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# ECOLOGICAL MONOGRAPHS

VOL. 25

JANUARY, 1955

NO. 1

OFFICIAL PUBLICATION OF THE ECOLOGICAL SOCIETY OF AMERICA

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## CONTENTS

### Some Feeding Patterns of Coyotes in Nebraska

Edson Fichter, George Schildman, and J. Henry Sather  
(Pp. 1-37)

### Vegetational Changes in the San Antonio Prairie Associated with Grazing, Retirement from Grazing, and Abandonment from Cultivation

John L. Launchbaugh  
(Pp. 39-57)

### Habits and Adaptations of the Great Plains Skink

Henry S. Fitch  
(Pp. 59-83)

### Ecological Relations of Jaegers and Owls as Lemming Predators near Barrow, Alaska

Frank A. Pitelka, Quentin Tomich, and George W. Treichel  
(Pp. 85-117)

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PUBLISHED QUARTERLY BY DUKE UNIVERSITY PRESS  
DURHAM, N. C., U. S. A.

# ECOLOGICAL MONOGRAPHS

A QUARTERLY JOURNAL  
FOR ALL PHASES OF BIOLOGY

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Agents in Great Britain: The Cambridge University Press, Bentley House, 200 Euston Road, London, N.W. 1. Prices can be had on application.

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Entered as second-class matter December 18, 1930, at the Post Office at Durham, North Carolina, under the Act of Congress of March 3, 1879.

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# SOME FEEDING PATTERNS OF COYOTES IN NEBRASKA<sup>1</sup>

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## TABLE OF CONTENTS

	PAGE		PAGE
INTRODUCTION .....	1	Mammals .....	13
EXTENT AND METHOD OF STUDY .....	3	Rabbit-mouse-pocket gopher Group .....	14
GENERAL CONDITIONS OF EXISTENCE IN NEBRASKA..	5	Rabbit .....	15
Topography .....	5	Mice .....	18
Climate .....	5	Pocket gopher .....	20
Vegetation .....	5	Muskrat .....	24
MAJOR LAND TYPES IN NEBRASKA .....	6	Deer .....	25
Western High Plains .....	6	Domestic mammals .....	27
Sandhills .....	6	Cow .....	27
Loess Hills .....	6	Birds .....	29
Loess Plains .....	6	Pheasant .....	29
Drift Hills .....	7	Grouse .....	32
STUDY AREAS .....	7	Domestic chicken .....	33
Nebraska National Forest: Bessey Division .....	7	Cold-blooded Vertebrates .....	33
Valentine Lakes Area .....	8	Insects .....	33
Loess Hills Study Areas .....	8	Fruit .....	34
COYOTE POPULATIONS IN NEBRASKA .....	9	Grass .....	34
Coyotes on the Study Areas .....	9	DISCUSSION .....	34
BASIC FEEDING PATTERN .....	9	SUMMARY .....	35
SPECIFIC FEEDING PATTERNS .....	13	LITERATURE CITED .....	36

## INTRODUCTION

Marked declines in populations of the ring-necked pheasant (*Phasianus colchicus*) during the middle of the last decade, notable throughout much of the bird's range in North America, was looked upon by many sportsmen in Nebraska as a result of predation. An abundance of coyotes (*Canis latrans*) apparently inspired a popular notion that responsibility for payment of bounties on coyotes should be shifted from the counties to the Game, Forestation and Parks Commission as an alleged mechanism for increasing the harvestable surplus of pheasants. Furthermore, an increase in the bounty rate by legislative action that became effective September 7, 1947, appeared imminent early in that year. Because of these circumstances, a study was undertaken by the Nebraska Game, Forestation and Parks Commission in an attempt to determine the effects of predation by coyotes on populations of the pheasant, and thereby to examine the justifiability of spending sportsmen's dol-

lars in a program of so-called coyote control as a means to better hunting.

Plans for the investigation envisioned its progression in two distinct phases, the first to be largely exploratory, involving studies on home range, population densities, behavior patterns, and foods of coyotes, i.e., details of the ecology of the predator, some knowledge of which was thought to be essential to effective prosecution of the second and possibly decisive phase. Scott (1943) states that "home range, movements and life history" of the red fox are importantly related to that predator's food interrelationships. The second phase of the study was to have hinged upon experimental efforts on large tracts of land with depressed populations of coyotes being the induced variable, similar to the studies of Edminster (1939) and Crissy & Darrow (1949) in New York state, and of Horn (1941) in California; measurements of populations of the predator and certain key species of prey were to have been included.

The investigation was initiated in February 1947, and discontinued as an organized project, with the

<sup>1</sup> Study undertaken with Federal Aid in Wildlife Restoration Funds under Nebraska Pittman-Robertson Project 15-R.



first phase still in progress, in June 1949. Some additional information was gathered until March 1952. Data gathered during this period of field and laboratory effort relate primarily to foods and feeding patterns of coyotes and, as such, shed little or no light on the problem which prompted the study; they do, however, appear to furnish certain indications which are interesting, if not significant, regarding coyote-prey relationships in general. In view of the suggestions that a "major step in evaluating the effect of a predator species on prey forms is to study the diet" (Craighead, not dated) and that comparison of the feeding trends of a predator in different habitats may be helpful in further understanding the role of predation in the natural community (Scott 1947), the present report is offered.

Our approach to the problem was predicated upon two premises: (1) That the *effects* (if any) upon the populations of one or more prey species by a given predator furnish the only criteria by which the predator may be intelligently judged in relation to human values; i.e., that the designers of wildlife management programs must be concerned with the fates of populations rather than with the fates of individuals as influenced by the species of predator in question. (2) That the role of a predator as a limiting factor impinging upon any prey species can probably be revealed reliably only by controlled experiments in the field over extended periods.

We were aware of evidence having been presented which suggests that predation may at times be without truly depressive influence because of intraspecific self-limiting mechanisms more effective in basically determining population levels maintained by a given prey population within a natural community (Errington 1946). Not without value in our contemplation of the problem was the concept that predation, by virtue of its universality, if nothing else, has, on the other hand, the appearance of an essential function in the total economy of the community. We were further cognizant that "experimental manipulation of vertebrate populations has been tremendously handicapped by technical and economic obstacles" (Errington 1946). It apparently still is.

More apropos this report is the conviction that information furnished by analyses of stomach contents, seats, den refuse, food caches, etc., can provide generally reliable indications only of the relative and shifting importance of prey species and other foods to the predator. Furthermore, much of such data can be misleading without the tempering influence of accompanying field observations; even when so interpreted, they are largely academic, and must be considered inconclusive, even deceiving, as evidence on which to base the design or promotion of management or "control" programs. Murie (1945) has clearly written that "the mere statement of a percentage of any item in the diet of a predator is no longer considered sufficient for economic evaluation." Information on the coyotes' feeding patterns was sought only because "general food habits studies

constitute a necessary groundwork for the more specialized research that may profitably follow" (Errington 1935).

It is not our purpose in this paper to exhaust the data at hand. Significant information on the food relationships of the coyote can be presented here without a comprehensive analysis of all data gathered. This plan of presentation is in keeping with our originally conceived objective of harmonizing the academic with the so-called "practical" approach to such a problem. It should be noted, however, that tabulations of all percentage values determined for representations of food and other items in droppings and stomachs are made available for whatever further analyses may be desired by others.

Many people helped make this report possible. According to records available, the following Nebraskans whose addresses were recorded, collected coyote stomachs: Ben Ammon, Bassett, Frank Barcal, Crawford, Floyd Daily, Leshara, Adolph Dirks, Johnson, Erlin G. Evans, Hayes Center, C. W. Gieser, Tecumseh, Claude Hamilton, Valentine, Ed Hashberger, Schuyler, Albert Herrmann, Eddyville, J. R. Holmes, McCook, Charles R. Hornolka, Loretto, Leroy Hurlburt, Arcadia, Ralph Ingles, Bloomfield, Ross Jackson, Oshkosh, Titus Johnson, Waverly, Wendell Johnson, Ceresco, C. N. Ogden, Lincoln, Wallace Peck, Grant, Joseph A. Proskovec, Malmo, Leo D. Riddell, Springview, Dick Shinn, Dunning, Walter Stammerjohn, Cairo, Elmer C. Sternhagen, Chadron, "Fuzzy" Stillwell, Valentine, and William E. Weigel, Beatrice. Other cooperators who collected stomachs but whose addresses were not recorded or whose first names or initials did not appear on the tags are: Ed Flynn, M. Gaskins, S. Richardson, F. Rieben, and Messrs. Gould, Munster, Sausman, and Thierion. Names on stomach tags were frequently difficult to read; we regret any misspellings or omissions. To all of these cooperators we are grateful.

We are indebted to the following employees of the Nebraska Game, Forestation and Parks Commission who were helpful in many ways: Supervisors William Cunningham and Lloyd Vance, Conservation Officers William Ahern, Robert Benson, Lee Bowers, Edward Cassell, L. J. Cunningham, A. O. Edmunds, Sam Grasmick, Clyde Grossoehme, H. B. Guyer, Lee Jensen, Don Lidolph, A. G. McCarroll, Roe E. Meyer, Roy E. Owen, Bernard Patton, William Schultz, Jack Strain, James Scott, and C. W. Shaffer, State Trappers Harold Miner, Dale Jones, and George Hytrek, and Planting Crew Foreman Cal Sampson.

The technical advice of Biologists Levi Mohler, David Damon, and John Wampole was indispensable.

The arduous task of laboratory analysis, accomplished by or under the supervision of Schildman, was lightened and research efforts strengthened in both field and laboratory by the able enthusiasm of Robert Anderson, J. Knox Jones, Jr., George Kelley, Bernard Leman, Dean Murphy, Robert Packard, and Olin Webb, all students at the University of Nebraska at some time during the period of our study.

To the following land owners and operators very special thanks are accorded for granting us permission to move freely on their farms and for many other courtesies: In Valley County, Walter Foth and son Lyle, Will Foth, Harry Foth and son Eldon, Theodore King, Archie Mason, Merle Page, Oscar Travis, and Laverne Aldrich; Frank and Russell Hackel, Walter Dobson, and Paul Lentz were also most helpful; in Greeley County, Sidney Allison. It is a special pleasure to acknowledge with gratitude the friendly co-operation of Al Cambell and George Wiseman of the Valentine National Wildlife Refuge, M. F. Brandborg, Ralph R. Hill, John Maslak, Ralph H. Schmalljohn, Carl Smith, and Russell Smith of the United States Forest Service, and Nobel Buell and Tom Turner of the Division of Predator and Rodent Control, U. S. Fish and Wildlife Service. Thanks are due pilots Howard Christensen of Scotia and Don Higgins of Ainsworth for skillful service in aerial reconnaissances.

The interest of Dr. H. T. Gier who was conducting a similar study at Kansas State College is deeply appreciated. We are especially indebted to E. R. Kalmbach and Charles C. Sperry, of the Denver laboratory of the Fish and Wildlife Service, without whose courtesies and technical advice our early efforts would have been hampered. Specific identification of many of the plants mentioned in the descriptions of vegetation was furnished by Dr. Walter Kiener, Aquatic Biologist with the Nebraska Game Commission.

The authors are indebted to Ardith Fichter for the typing of the manuscript. To those persons who were in any way helpful, but whose names have inadvertently been omitted, our thanks and our apologies.

#### EXTENT AND METHODS OF STUDY

This report is based upon the examination of 2,500 coyote seats and of the contents of 747 of 844 coyote

stomachs collected in Nebraska during the 50 month period January 27, 1947 to March 20, 1951. Distributional and other background data concerning these sources of information are given in Tables 1 and 2. Most of the seats were collected by the authors. In the field, each seat considered to be a unit dropping was placed in a small paper sack upon which locality and date of collection were indicated. An effort was made to include any other pertinent information, such as (1) the relative age of the seat, i.e., whether fresh, recent, old, or very old, (2) proximity to known carrion or breeding den, (3) outstanding features of habitat, terrain, fauna, or weather, (4) association with known "scatting" stations, (5) if a pup seat, or (6) of questionable identity.

Most of the stomachs were collected by coyote hunters; some were secured by employees of the Game Commission, including the authors. Efforts were made to secure for each stomach a record of the locality and date of kill, the method by which the coyote was taken, and the age of the animal, i.e., whether pup, young of the year, or adult. Collectors were equipped with cheesecloth, string, tags, formalin in 10-gallon milk cans, and directions for collecting stomachs. It seems significant to note that, of 14,829 coyote stomachs collected for examination at the Denver Laboratory of the Fish and Wildlife Service over the five-year period 1931-1935 by fieldmen (Sperry 1941), 13.6% were considered empty and 29.4% contained "debris only," and that a comparable percentage (11.5%) of the 844 stomachs secured for the present study were empty, whereas less than 1% contained debris only. This latter marked discrepancy probably relates to the methods by which the coyotes were taken, only about 2% of the stomachs at our disposal having been collected from coyotes taken in traps. The advantages of "sudden death"

TABLE 1. Areal distribution, reported methods of take, and volume of contents of 844 coyote stomachs collected in Nebraska from January 27, 1947 to February 4, 1949.

Method of take	Western plains	Sand-hills	Loess hills	Loess plains	Drift hills	Mixed land types	Without data	Pup stomachs	All
Shooting*	1	26	103	22	8	23	0	0	183
Cyanide gun	24	2	66	19	3	11	0	0	125
Airplane	3	3	22	0	37	4	0	0	69
Dead on road	0	1	0	0	0	0	0	0	1
Roundup	0	0	24	101	12	7	0	0	144
Dogs	0	21	22	2	6	17	0	0	68
Den digging	1	0	2	4	0	0	0	38	45
Trap	3	6	1	0	4	2	0	0	16
Not reported	0	18	28	5	23	11	11	0	96
Totals usable	32	77	268	153	93	75	11	38	747
Empty	5	5	36	18	18	11	3	1	97
GRAND TOTALS	37	82	304	171	111	86	14	39	844
VOLUME OF CONTENTS (cc)	6,755	14,686	60,371	42,545	24,259	17,858	1,540	2,751	170,765
AVERAGE VOL. OF CONTENTS	211	191	225	278	261	238	140	72	229
Excluding pup stomachs	...	...	...	...	...	...	...	...	238

\*Many coyotes reported as having been taken by "shooting" were probably shot from airplanes.

TABLE 2. Areal and seasonal distribution of 2500 coyote seats collected in Nebraska from February 26, 1947 to March 20, 1951.

	Winter	Spring	Summer	Autumn	All
<b>STUDY AREAS</b>					
<i>SANDHILLS</i>					
Nebraska National Forest.....	912	572	176	80	1740
Valentine Lakes area.....	277	126	0	16	419
Totals.....	1189	698	176	96	2159
<i>LOESS HILLS</i> .....					
	41	102	28	23	194
<b>SCATTERED LOCALITIES</b>					
Pup seats.....	0	58	0	0	58
Others.....					89
GRAND TOTALS.....	1230	858	204	119	2500

of the predator in gathering such material for study becomes obvious.

Each seat was first soaked in water in a quart jar, then churned in the water by means of a device which tumbled the jar; the thoroughly separated materials of the seat thus treated were dumped into a screen-bottomed tray over a shallow pan of clean water. Proper manipulation of the screen into and out of the water made possible a detailed examination which we consider reliable in disclosing remains of all food items represented.

The total contents of each usable stomach were measured volumetrically by water displacement in a graduated cylinder. All items represented were separated, identified, and, excepting parasitic worms, measured volumetrically. Percentages of both occurrence and volume were thereby calculable for items appearing in the stomachs. A representation too small to be measurable was recorded as a trace, "T" in the tabulations.

Frequencies of food and other items in both stomachs and seats are expressed as percentages of occurrence, i.e., the percentage of stomachs or seats in which the items occurred (Tables 4, 5, and 7 to 11). Relative volumes of the various items in stomachs are expressed as percentages of volume (Tables 4, 6). Where adequate collections were available, these data are categorized on the basis of land type (Tables 5, 6, 8, and 9) and season (Tables 7 to 10 inclusive). Values furnished by analysis of seats are not lumped with those furnished by analysis of stomach contents. Data gathered from these two sources are, however, considered to be correlative and mutually supportive.

It must be remembered that the number of occurrences of a given prey item in the seats of a predator cannot routinely be interpreted as indicating that the same number of individuals was ingested. Scott (1943) has furnished experimental evidence that the "number of occurrences in fox seats resulting from a specific food appears to vary somewhat in direct proportion to the amount eaten," and reports "a large meadow mouse averages one to two occur-

rences, whereas a meal of domestic chicken may result in as many as 15 or more occurrences." Murie (1946) has concluded, by virtue of experimental feeding of captive coyotes, that where a record of the actual number of individual prey animals eaten is sought by way of seat analysis, "there probably is slight chance of duplication in the total tally of prey, up to the size of a squirrel, or even of a marmot," but that "the number of mice listed would likely be under the true figure."

Because of the differential in the potential number of occurrences furnished by prey species or carrion sources of different size, and because analyses of stomach contents and seats cannot disclose the effect of the coyote upon *populations* (numbers) of prey, evidence of actual numbers of prey animals consumed is not sought in the data presented here. Times of occurrence are not treated as individuals. It is not necessary, therefore, to arbitrarily give such items as insects an expression different than that afforded remains of vertebrates, although the two may not be readily comparable. Since this exploration into the feeding habits of the coyote in Nebraska was planned only as a source of possible guides to experimental efforts, percentage occurrence was looked upon as an index to *dependency* upon food groups and items and, thereby, to some extent, as an index to the areal and chronological *pattern* of predation pressure afforded various food groups and items by the coyote.

While coyote stomachs were received from collectors throughout much of Nebraska, special efforts to secure study materials from areas of denser pheasant populations (Anonymous 1946) resulted in 56% of the 747 usable stomachs being taken in the loess hills and plains regions (Fig. 1) which encompass what has been popularly called the state's "pheasant belt." Inasmuch as most of the stomachs were secured in winter, some seasonal bias probably appears in the data. Difficulty in finding droppings of coyotes in loess farmlands, even though the animals were abundant there, and marked opportunity for securing seats in large numbers in certain situations in the sandhills, resulted in concentration of seat collecting in two strikingly different areas within this latter land type, namely, the Bessey Division of Nebraska National Forest in Thomas and Blaine counties, and what is referred to here as the Valentine Lakes area including the Valentine National Wildlife Refuge and adjacent Ballard's Marsh in Cherry County (Fig. 1). Intensive collecting and observations were also effected on two study areas in the loess hills, one of about 3 sq. mi. in Valley County, the other of 1 sq. mi. in Greeley County (Fig. 1).

The coyote may owe some of its success as a species to its faculty for crossing many ecotones. The data gathered here make possible a comparison of some of this "predator's feeding trends in markedly different habitats" (Scott 1947) and may, it is hoped, serve to add to man's increasing knowledge of the role of predation in the total economy of the biotic community of which, man must learn, he is inescapably a member species.



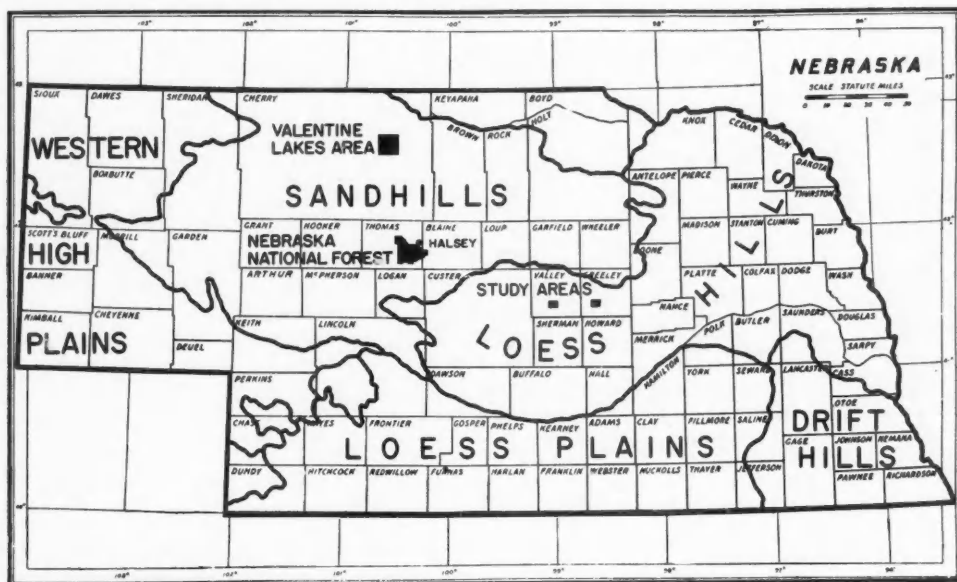


FIG. 1. Map showing the major land types in Nebraska. (Generalized)

#### GENERAL CONDITIONS OF EXISTENCE IN NEBRASKA

The following brief account of general environmental conditions in Nebraska is based upon Pool (1912), Aikman (1929), Weaver and Clements (1938) and Anonymous (1941).

##### TOPOGRAPHY

Nebraska lies wholly within a major physiographic division known as the Interior Plains. The greater part of the state comprises a part of the Great Plains; at the eastern end of the state a strip averaging 70 mi. in width lies within the Central Lowland Province. Nebraska's expansive, gently rolling to rough topography is largely characterized by low hills, occasional isolated buttes, ravines, narrow canyons, broad, level stream valleys, and several relatively shallow east-flowing streams. The surface of the state slopes gently southeastward. The highest elevation of 5,430 ft. is in Banner County, in western Nebraska, and the lowest point of 835 ft. is in the extreme southeastern corner of Richardson County.

##### CLIMATE

The climate of Nebraska, characterized by comparatively short, hot summers, long, cold winters, and fluctuating rainfall, results from its geographic location near the center of the continent. The state has two rather well-defined climatic belts—subhumid east of the 100th meridian, semiarid west of it, with a transitional zone between. Precipitation decreases from east to west across the state at a fairly constant rate. The mean annual precipitation is generally less than 20 in. west of the 100th meridian and more than 20 in. east of it. Annual precipitation varies from

9.47 in. to 27.48 in. in western Nebraska, and from 20.86 in. to 50.31 in. in eastern Nebraska.

##### VEGETATION

Nebraska lies wholly within the grassland climax; forest formations occur, however, at both the eastern and western ends of the state. The grassland formation was natively represented in the state by the true prairie in the east and the mixed prairie in the west, with transition from one to another being gradual over a broad ecotone. Tall grass prairie occurs as a post-climax to the true prairie, notably so in the sandhill complex of north-central Nebraska. Where overgrazing has favored the dominance of the short grasses, the mixed prairie has given way to a short grass disclimax, especially in the west. Cultivation has removed most of the true prairie and much of the mixed prairie within the state.

The deciduous forest formation is represented in Nebraska by the oak-hickory association, largely along the Missouri River and its tributaries bordering which deciduous forest reaches far into the prairie. Red oak and linden are the climax dominants in this western outpost of the formation, showing close topographic association. Woodland natively extended uninterruptedly over hilltops several miles from the Missouri River. The distribution of continuous forest vegetation is limited to the most sheltered sites in northeastern Nebraska. Cutting has everywhere reduced the extent of deciduous forest in the state, it now being confined largely to the rougher land.

Somewhat more extensive forest is found in northwestern Nebraska where the montane forest formation is represented by the consociation of *Pinus ponderosa*. Where the rolling, natively grass-covered

plains suddenly give way to a topography characterized by deep, rocky canyons and eroded buttes, western yellow pine is the most evident tree, growing in scattered stands on the steep slopes and forming the open forest characteristic of this species. Elements of the deciduous forest formation occupy much of the canyon floors. Both coniferous and deciduous forest representatives reach into the prairie in the form of savannah, the yellow pine along the ridges and steep slopes, the deciduous trees along the streams. These vegetational features can be found most strikingly expressed in and associated with the Pine Ridge, a rocky escarpment entering Nebraska at its northwest corner and extending as a narrow tongue of rough land about halfway across the northern portion of the state; they also occur along the Niobrara River and in the comparable rough lands in southwestern Nebraska. Coniferous forest areas in the state are used largely for grazing of cattle, lumbering apparently having never been of marked importance.

#### MAJOR LAND TYPES IN NEBRASKA

As one approach to this comparative study of the feeding patterns of the coyote under various conditions in Nebraska, the five major land types within the state are broadly treated as five more or less different, albeit extensive habitats; values relating to foods of coyotes, as furnished by analyses of stomach contents and seats, are categorized under the various land types (Tables 5, 6, 8, and 9). It has been shown that land use, which is in considerable measure an expression of land type, "has a strong influence on the kinds and populations of wildlife" (Albrecht 1943). The implication that populations of potential prey for the coyote, including the pheasant (Anonymous 1946), may be one of the ultimate expressions of land type, suggests this approach. Such an areal grouping of our data might be based with more ecological significance upon biotic regions *per se*. Unfortunately, no satisfactory treatment of biotic regions within Nebraska has been produced. In this respect, it is noteworthy that five "faunal regions" briefly defined for the state by Wolcott (1906) show remarkably close correlation with its major land types. It must be clearly understood, however, that the land types as delineated (Fig. 1) and described for the purposes of this study are considerably generalized; they have been delineated previously in like manner (Fichter & Jones 1953).

#### WESTERN HIGH PLAINS

That area of Nebraska referred to in this report as the western high plains occupies the extreme western part of the state west of the sandhills and the loess plains, and is separated from the latter land type largely by sandy outliers that extend southwest from the larger sandhills region proper. Topography is level to hilly and broken, characterized by (1) high, arid tablelands, (2) the pine-clad Wildcat Hills and associated rough lands south of the Platte River Valley, (3) "rimrock" buttes and promontories such

as those bounding the valleys of the Platte and Niobrara rivers, (4) scattered, relatively small patches of sandhills, (5) the north-facing, deeply dissected sandstone escarpment of the Pine Ridge to the north with yellow pine on the steep slopes, and (6) scattered badlands produced by water erosion. Grazing, mostly by cattle, and wheat farming constitute the principal land uses in this type. Intensive cultivation is practiced under irrigation principally in the Platte Valley, with emphasis on alfalfa, potatoes, and sugar beets.

#### SANDHILLS

Approximately 20,000 sq. mi. of north-central Nebraska are occupied by dune sand and extremely sandy soils in a monotonous succession of sandhills and ridges, swales, and valleys (Fig. 2). The open sandhills are mostly captured under a cover of grasses, postclimax tall grasses, in part, because of the ready absorption of precipitation and high percentage of available water. Some relatively small areas of moving dunes exist and "blow-outs" are not uncommon, especially where overgrazing or excessive trampling by cattle are allowed. Shrubs are conspicuous in pockets in the hills, with an occasional lone hackberry tree or hackberry thicket showing. There are both dry and wet valleys, the latter especially in the northern and western portions of the sandhills where hay flats, sloughs, marshes, and lakes are conspicuous and biotically important features (Fig. 4). Except locally, this region of dune sand and associated sandy soils is suited only to grazing and production of "wild" hay. Utilization of the land here depends almost entirely upon preservation of the grass cover. The largest cattle ranches of the state are located in this great grassland area.

#### LOESS HILLS

This land type as projected here includes all of Nebraska east of the sandhills and north of the Platte River. In addition to the loess hills proper, characterized by soils largely identical with those of the loess plains but with a generally rougher topography (Fig. 5), we are including with this type the nearly level to strongly rolling country of northeastern Nebraska over much of which glacial drift is mantled by loess-derived soils. In all, it is an area marked by many major streams draining from the sandhills which border it on the west. Here the production of oats, rye, barley, and corn supports an agricultural economy. Areas of deciduous forest occur in the rougher land along the eastern and northern edges of this land type.

#### LOESS PLAINS

Occupying much of Nebraska south of the Platte River are the nearly level to gently rolling loess plains. On the eastern margin they merge into the area of glacial drift. This plains area is characterized by loess-mantled uplands, now largely cultivated and producing, for the most part, sorghum, corn, and small grains, especially winter wheat.

## DRIFT HILLS

Characterized by hills formed of glacial drift, the drift hills land type, as here defined, lies east of the loess plains and south of the Platte River and includes a relatively narrow southward extension of the loess-on-drift of northeastern Nebraska. Some of the drift hills are thinly strewn with boulders and some are deeply gullied, but generally their surfaces are comparatively smooth. Many stream valleys contribute to the broken topography, and some uplands and hills are capped with loess. Corn, winter wheat, oats, and alfalfa are grown in this land type.

In addition to the deciduous forest features of this region, briefly described in the account of native vegetation, the drift hills are also characterized by many and expanding orchards and by hundreds of miles of osage orange hedge rows. The latter, unfortunately, have become unpopular with land operators in recent years, and are suffering removal (Harmon & Damon 1947).

## STUDY AREAS

## NEBRASKA NATIONAL FOREST: BESSEY DIVISION

The Bessey Division of Nebraska National Forest is an area of 90,388 ac of typical Nebraskan sandhills, located in southeastern Thomas County and southwestern Blaine County near the southeastern border of the sandhill region (Fig. 1). Two boundaries of the roughly triangular reserve rather closely parallel the Middle Loup and Dismal rivers.

The native vegetation of the tract (Fig. 2) appears to conform predominantly to the dune sand type of Frolik & Shepard (1940) and others. In their survey of the vegetative composition and grazing capacity of sandhill range land in a grazed area about 40 mi north of the Bessey Division in 1937, these authors found this vegetative type occurring "on the dune sand throughout" all of the sandhill areas having a rolling or choppy topography. Their report states: "The characteristic aspect of the dune-sand type is due largely to *Calamovilfa longifolia*, but it is somewhat modified by *Sporobolus cryptandrus*. Although unobtrusive in appearance, *Bouteloua hirsuta* ranks second to *Calamovilfa* in percentage of ground covered. These three are the most important constituents of the type and together make up nearly 70% of the total grass density." They also report that "shrubs often occupy a conspicuous place in the general aspect of the dunes, even though contributing only 7.7% of the density," and that forbs "comprised 13.3% of the vegetative density during 1937."

Small stands of hackberry (*Celtis occidentalis*), cottonwood (*Populus deltoides*), choke cherry (*Prunus melanocarpa*), and wild plum (*Prunus americana*) occur natively. The cherry and plum are commonly found forming thickets of shrubs or small trees, often associated with buckbrush (*Symphoricarpos occidentalis*), wild rose (*Rosa arkansana*) and the shrubby upland willow (*Salix humilis*). Redroot (*Ceanothus ovatus*) and the sand cherry (*Prunus besseyi*) are important shrubs throughout



FIG. 2. Sandhills in the southern portion of the Bessey Division of Nebraska National Forest, looking slightly south of east and showing the monotonous succession of the grass-captured dunes, something of the nature of the woody vegetation, and a part of the road along which coyote scats were gathered. Photo by Levi Mohler.

this grassland. Green ash (*Fraxinus pennsylvanica*) occurs natively in the river valleys, associated there with cottonwoods and willows.

Planting of conifers on Nebraska National Forest was begun in the spring of 1903. The Bessey Division now contains more than 30,000 acres of growing evergreen trees (Fig. 3). Jack pine (*Pinus banksiana*) plantings are the oldest, with some of the trees exceeding 40 ft. Western yellow pine has been the most successful pine. Recent plantings have emphasized the eastern red cedar (*Juniperus virginiana*) which is a native of the general region and grows the most successfully of the evergreens.



FIG. 3. View to the north in the northwestern portion of the Bessey Division of Nebraska National Forest showing some of the older plantations of conifers and the gravelled road along which many coyote scats were collected.

Forage within the Forest Reserve is utilized by the allotment of grazing permits to neighboring ranchers, except where the presence of cattle would interfere with forestation operations.

The selection of this tract, where pheasant numbers are very low, as a study area relating to an investigation of coyote-pheasant relationships, might at first



seem questionable. The choice seemed advisable, however, because (1) coyotes were present in good numbers, (2) efforts to secure coyote seats were very fruitful, (3) the population of sharp-tailed grouse (*Pediocetes phasianellus*) appeared to be representative of that over much of its range in the sandhills at that time, (4) a herd of 300 or more mule deer (*Odocoileus hemionus hemionus*) was resident on the Forest (Mohler, Wampole, & Fichter 1951), (5) the presence of coniferous forest plantations of many ages and their juxtaposition to native grassland out of which they are rising as a result of a grand biological experiment, and not the least important, (6) primitive conditions are probably closely approximated over much of the remainder of the tract. The desirability of studies in primitive areas has been repeatedly emphasized. The desirability of studies within the plantations of Nebraska National Forest cannot be over-emphasized.

Fifteen to 20 mi of narrow work-road within the Bessey Division were graded and gravelled in the 1930's (Figs. 2 and 3), and continue to be maintained. Many miles of truck trails branch from the improved road. Early in our observations it became evident that coyotes were traveling the gravelled thoroughfare and dropping many seats upon it, in many places at what appeared to be regularly visited scatting stations. Several such stations were associated with junctions of the gravelled road with truck trails. Because the coyote droppings could be easily seen along this road, it was possible (1) to find them while cruising slowly in a car or truck, thereby collecting many in a relatively short time over the entire length of road, and (2) to secure all of the seats along a three-mile ("scat-run") segment of the road, selected for intensive effort, by walking it in both directions. Such intensive collecting made possible reasonably accurate timing of seat deposition and contributed importantly to a seasonal breakdown of data thereby gathered.

#### VALENTINE LAKES AREA

In certain portions of the sandhills of Nebraska, especially in the north and west, lakes, marshes, and wet meadows (Fig. 4) occupy many of the valleys and furnish conditions of existence markedly different than those found in such uniformly xeric situations as represented by the Bessey Division of Nebraska National Forest. Typifying this interspersion of xeric and hydric habitats is the Valentine Lakes Area in Cherry County and some fifty airline miles north of the Bessey Division. Efforts relative to this report were much less intensive here than on the National Forest and included direct observations on coyotes and the collecting of their droppings, mostly by Sather in conjunction with his intensive studies on muskrats from the fall of 1948 through the spring of 1952.

The Valentine Lakes Area as designated for the purposes of this study is comprised of the Valentine National Wildlife Refuge plus Ballard's Marsh just outside the Refuge to the north. Sather's investiga-



FIG. 4. Winter aspect of wet meadow and willow marsh in Valentine National Wildlife Refuge, with grass-covered sandhills beyond.

tions on muskrats involved Rice, Pony, Center, "21," Sweetwater, and East Twin Lakes, the Marsh Lakes—North, Middle, and South, and West Long Lake within the Refuge; his direct observations on coyotes were made largely on Ballard's Marsh and its environs.

The composition of the vegetation of this area has been described by Frolik & Shepard (1940) with special attention to livestock carrying capacity. Five "major range types of grassland . . . were identified and designated" (1) dune sand vegetation, (2) dry valley or bunchgrass of dry meadows, (3) wet phase of tall-grass meadows, (4) dry phase of tall-grass meadows or transition type, and (5) salt grass or alkali meadows. These authors designated non-forage, hydric vegetation as "marsh." Tolstead (1942) reports the chief aquatic plants as being species of *Potamogeton*, *Myriophyllum*, *Ceratophyllum*, *Typha*, *Sagittaria*, *Scirpus*, and *Phragmites*, with *Distichlis stricta* and *Scirpus americanus* growing on the shores and in the saline meadows. Mesophytic tall-grass communities in subirrigated meadows are described by Tolstead as occurring in three zones. A lower zone, usually flooded during the spring, is occupied by various sedges (*Carex* spp.) and hydrophytic grasses, chiefly *Calamagrostis*. A middle zone is never flooded but water is near the surface throughout the year, and here the tall grasses *Spartina pectinata*, *Panicum virgatum*, *Sorghastrum nutans*, and *Andropogon gerardi* are dominant. The upper edge of the meadow is dominated by true-prairie grasses. Dr. Walter Kiener indicates that the willow occurring extensively in the marshes and dominating the shrubby cover is *Salix gracilis*.

#### LOESS HILLS STUDY AREAS

About 75 airline mi east-southeast of the Bessey Division and 130 mi from the Valentine Lakes Area was located the Valley County coyote study area (Fig. 5), and 25 mi east of that, the Greeley County study area. These comprise duplicate areas in the loess hills land type and will thenceforth be treated together as representative of this region of rolling agricultural lands, steep slopes, eroded steep-sided canyons, and level-floored valleys. Cultivation of the valley floors is intensive with corn, wheat, alfalfa, and sweet clover being produced. These same crops are being raised on some of the tillable uplands; much of



FIG. 5. Winter scene in the loess hills land type looking northeast across Mira Creek valley from within the Valley County coyote study area, showing the pattern of cultivation, the dissected nature of the rough lands, and the occurrence of native vegetation. Photo by Levi Mohler.

the hill land is in pasture, with many of the pastures being heavily grazed if not overgrazed by cattle.

Small areas of native vegetation continue in a few places. Blue-grass frequently appears to be the dominant grass, with ash, cottonwood, chokecherry, wild plum, and buckbrush characterizing the woody vegetation. Shelterbelts are conspicuous features of the landscape here.

In these loess hills areas, studies of coyote behavior were intensive (Fichter 1950). Efforts to secure seats were much less fruitful than in sandhills situations. Coyotes were apparently equally abundant in the two types—possibly more abundant in the loess hills—but more intensive use of the land by man in the latter plus the heavier vegetational cover made the droppings more difficult to find. A few definite scatting stations were found, mostly in pastures.

#### COYOTE POPULATIONS IN NEBRASKA

Although there is good reason to believe that the bountying of any predator is subject to many variables and that the number of coyotes bountied in any given county is not necessarily the number taken in that political subdivision, bounty records do furnish an index not elsewhere available. In July 1951, a form was sent to each county clerk in Nebraska on which a tabulation of the number of bounties paid on coyotes in each month from 1941 through 1950 was requested. Data relative to the years 1948 through 1950 were received from 70 of the 93 counties. During those three years, immediately following the advent of the mandatory \$2.50 bounty per coyote and while our study was in progress, those 70 counties, comprising 58,653 sq mi or approximately 76% of the state's total area, paid bounties on 67,639 coyotes—an annual average of one coyote for every 2.6 sq mi of land, or 38.4 coyotes for every 100 sections.

A comparison of bounty data available for categorization on the basis of land type shows the number of coyote bounties per 100 sq mi virtually the same throughout the loess hills, loess plains, and drift hills, i.e., 45, 48, and 49, respectively. This index de-

creases to the west, 29 and 16 bounties per 100 sections being paid in sandhills and high plains, respectively. A breakdown of the loess hill data into those for loess-on-drift hills and loess hills proper reveals respective values of 24 and 69 bounties per 100 sq mi of land. These values may indicate with some reliability that coyotes were more abundant in the loess hills proper than to the northeast, east, and south. They cannot be accepted as proof that coyotes were less abundant in the sandhills and high plains. In these latter land types, human populations are less dense; it may be that there is consequently less frequent contact between men and coyotes, resulting in a smaller percentage of whatever population is present being taken for bounty. An index value of 69 coyotes bountied per 100 sections does point to a relatively dense population. The six loess hills counties that furnished the information from which this index value was derived are thought to be far enough from any state line that traffic occasioned by either higher or lower bounty rates was negligible.

#### COYOTES ON THE STUDY AREAS

It seems reasonably sound to report that coyotes were abundant on the study areas; the areas were selected with that status as one criterion requisite to a study of coyote pressures on pheasant. It was possible in the spring of 1948, for example, to remain in one spot on a hill in the Valley County area and effectively watch with binoculars the vicinity of three active coyote breeding dens. Valley and Greeley counties, both of which began paying bounties on coyotes late in 1947, report bountying 1,021 coyotes in 1948, 873 in 1949, and 800 in 1950—an annual average of one coyote for each 1.3 sq mi or 78.4 coyotes for each 100 sq mi.

Coyotes are and have been for many years rather numerous within the Valentine National Wildlife Refuge. Coyote control activities carried out during the winter months result in an annual take of about 100 animals. It is not at all unusual to see coyotes, and they can be heard almost any night. Cherry County, which had not paid bounty on coyotes before October 1947, reports bountying 1,189 coyotes in the calendar year 1948, 1,565 in 1949, and 2,288 in 1950, an annual average of one coyote for every 3.5 sq mi or 27.7 coyotes per 100 sections for that three-year period.

Estimates by Forest Service personnel placed the population of coyotes on the Bessey Division at 400 in 1948, 450 and "increasing" in 1949, and "increasing" but without numerical expression in 1950. On the basis of the lowest figure, the population of coyotes per 100 sq mi on this tract would have been 283, or nearly three per section. Blaine and Thomas counties bounty an annual average of 38.4 coyotes per 100 sections during the years 1948 to 1950, inclusive.

#### BASIC FEEDING PATTERN

Coyotes are primarily carnivorous, feeding largely upon the flesh of vertebrate animals. Cold-blooded

vertebrates (fish, amphibians, and reptiles) appear to be relatively unimportant quantitatively in the coyote's diet. The warm-blooded vertebrates (birds and mammals) comprise this carnivore's principal supply of food. Substantial quantities of insects and plant materials are eaten, however, the latter being largely grass and fruit. Grass passes through the alimentary tract of the coyote apparently undigested and is, therefore, not here considered to be a food as such, although it occurs more frequently than fruit. Fruits appear to serve the animal as digestible foods.

Data presented here suggest that the basic feeding pattern of the coyote can be expressed in terms of major food groups, a designation used by Scott (1943, 1947). In the present report, "major" indicates only quantitative importance; it may, but does not categorically imply ecologic importance of comparable magnitude. The word "group" is applied to any lumping of food items, taxonomic or arbitrary, and without virtue of reliable correlative data regarding ecologic significance.

Four major food groups are evident—mammal, bird, insect, fruit—categories essentially in agreement with those of Scott (1943, 1947), and with those implicit in information on the coyote's food habits furnished by Murie (1935, 1945), Bond (1939), and Sperry (1941). These four food groups, stated here in order of decreasing quantitative importance based on percentages of both occurrence and volume, and so expressed graphically in Figs. 6 and 7, may be thought of as comprising the *basic feeding pattern* of the coyote.

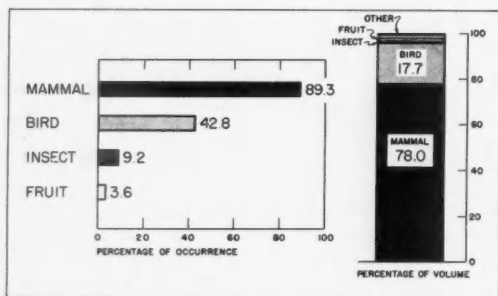


FIG. 6. Percentages of occurrence and volume of major food groups in 747 coyote stomachs collected in Nebraska.

The basic feeding pattern is, of course, subject to modification. The relative proportions of the major food groups may show marked variations from area to area (Figs. 8, 9, 10, and 11) and from time to time (Figs. 12, 13, and 14). These areal (geographic or local) differences and seasonal trends or shifts are thought to be reflections of differences in environmental conditions expressed for the most part through the function of *availability* of foods (see discussion).

The mammalian food group dominates the basic feeding pattern, whether ascertained in terms of frequency of occurrence in stomachs (Fig. 6) or in

droppings (Fig. 7), or as percentage of total volume of stomach contents (Fig. 6). Regardless of geographic coverage or variations in methods of study or expression of findings, it appears that a preponderance of mammalian remains universally characterizes the representations of food items in stomachs and seats of coyotes. Sperry (1941) pointed to this consistent pattern with his statement that coyotes throughout 17 western and midwestern states "depend on mammals for more than nine-tenths of their sustenance."

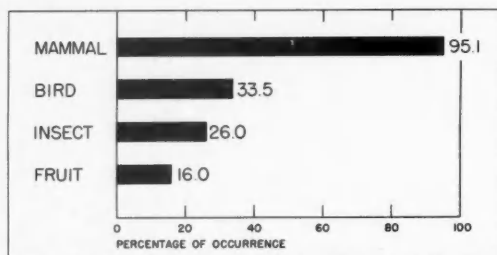


FIG. 7. Percentages of occurrence of major food groups in 2,500 coyote seats collected in Nebraska.

The marked dominance of the mammalian food group was consistent in coyote stomachs from the five land types in Nebraska, frequency ranging from 86.9% in stomachs from loess plains to 90.6% in those from the sandhills (Fig. 8). A somewhat greater range was shown by mammalian remains in percentages of total volume, from 67.9% in stomachs from loess plains to 92.4% in those from drift hills (Fig. 9). Values of frequency and volume of the mammalian food group were most closely approached by those of the avian group in stomachs from loess hills; even here remains of birds appeared in only 57.7% as many stomachs as did mammalian items (Fig. 8), and comprised but 30.0% of the warm-blooded vertebrate material (Fig. 9).

Values furnished by seats likewise demonstrate a preponderant frequency of mammalian remains in both sandhills and loess hills (Figs. 10 and 11).

The coyote's dependence upon the mammalian food group is evidently perennial with relatively slight variations (Figs. 12, 13, and 14) despite obvious, albeit largely unmeasured seasonal shifts in environmental conditions.

Birds constitute a food group apparently much less important than the mammalian group to the coyote (Figs. 6 and 7). It is noteworthy, however, that our findings in Nebraska appear to indicate a somewhat greater dependency upon the avian food group, at least during the period of our investigations, than has been reported in studies elsewhere. Sperry (1941), who expressed the frequency of food items in stomachs on the same basis as used here, found that birds occurred in 13.0% of 8,339 stomachs and contributed 2.92% of the total volume of contents. Bird remains were found in 42.8% of the 747 Nebraskan coyote stomachs and comprised 17.7% of the total volume.



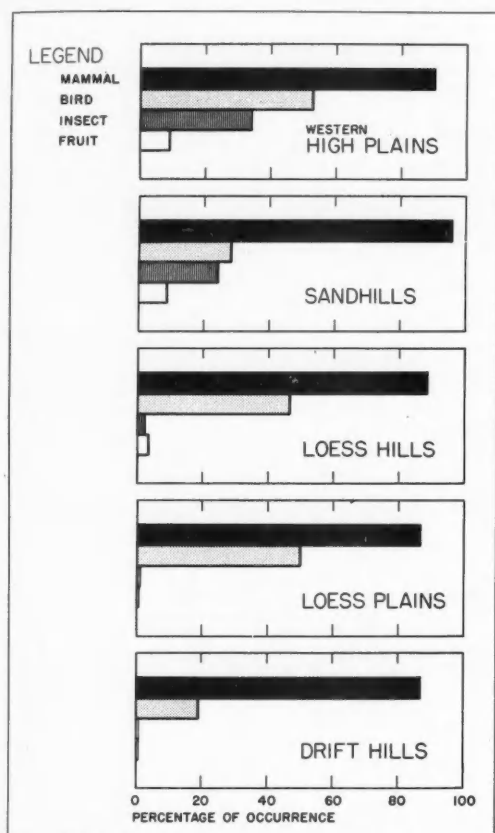


FIG. 8. Percentages of occurrence of major food groups in 623 coyote stomachs from five land types in Nebraska.

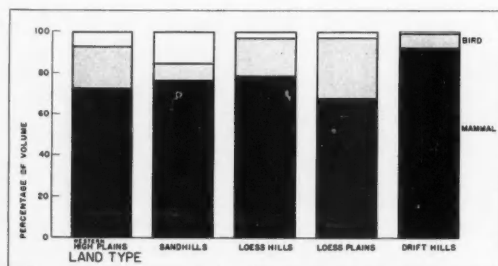


FIG. 9. Percentages of volume of avian and mammalian remains in 623 coyote stomachs from five land types in Nebraska.

Murie (1940, 1945), expressing frequency of food remains in coyote seats as percentage of total occurrences of all items, reports percentages for the avian food group ranging from 3.16% in 5,086 seats taken in Yellowstone Park to 12.9% in 67 seats collected along the breaks of the Missouri River above Fort Peck, Montana. Lumping Murie's data from Fort Peck, Sun River, and Flathead River in Mon-

tana, interior British Columbia, and Yellowstone, 5,770 seats yielded a total of 9,793 food item occurrences, 343 or 3.5% of which were bird remains. Table 3 shows a total of 7,336 food item occurrences in 2,500 Nebraskan seats, of which 858, or 11.7% were occurrences of bird. These 858 avian items occurred in 33.5% of the 2,500 seats (Fig. 7).

TABLE 3. Summary enumeration of food item occurrences by groups in 2500 coyote seats and 747 coyote stomachs collected in Nebraska from January 27, 1947 to March 20, 1951.

Food group	NUMBER OF OCCURRENCES		
	In 2500 seats	In 747 stomachs	Totals
MAMMAL			
Small wild.....	3379	863	4242
Large wild.....	191	3	194
Domestic.....	737	183	920
Undetermined.....	156	29	185
Totals.....	4463	1078	5541
BIRD			
Wild Galliformes.....	398	124	522
Other wild and undetermined.....	432	117	549
Domestic.....	28	106	134
Totals.....	858	347	1205
Other* and undetermined vertebrate material.....	165	42	207
Egg shell.....	89	2	91
INSECT**.....	649	69	718
PLANT MATERIAL†.....	1112	289	1401
GRAND TOTALS...	7336	1827	9163

\*Snakes, lizards, turtles, frogs, and fish.

\*\*All insect remains in any given stomach recorded as one occurrence.

†Excludes plant material interpreted as debris.

The coyote's degree of dependence upon the avian food group is apparently subject to great variation from place to place and from time to time. Figure 8 shows the percentage of occurrence of bird in stomachs ranging from slightly less than 20% for the drift hills to 53% in the western high plains; in Figure 9, percentages of volume are depicted ranging from 7.3% in stomachs from drift hills to 29.3% in those from loess plains. Incidence of bird remains in seats likewise shows marked differences from area to area (Fig. 10).

Somewhat less radical are the seasonal variations in consumption of birds as evidenced by their remains in seats (Figs. 12, 13, and 14). Most striking here (Fig. 13) is the seasonal pattern in the loess hills where, by virtue of a relatively high incidence of avian remains and a marked autumnal decline in the frequency of mammalian remains, these two major food groups register the same autumnal percentage (65.2%) of occurrence.

Areal and seasonal variations of even greater magnitude than those shown by bird remains are char-

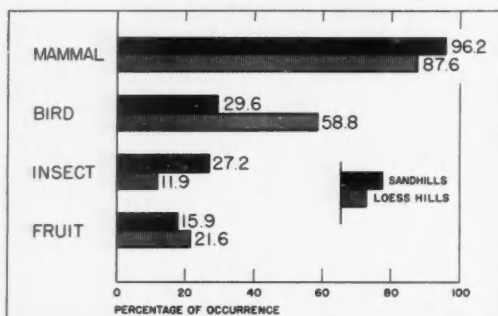


FIG. 10. Percentages of occurrence of major food groups in 2,159 coyote seats collected in sandhills and in 194 seats taken in loess hills.

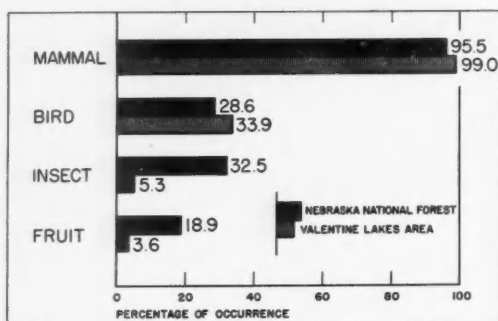


FIG. 11. Percentages of occurrence of major food groups in 1,740 coyote seats from a xeric sandhills habitat (Nebraska National Forest) and in 419 seats from an area of lakes and marshes in the sandhills (Valentine Lakes Area).

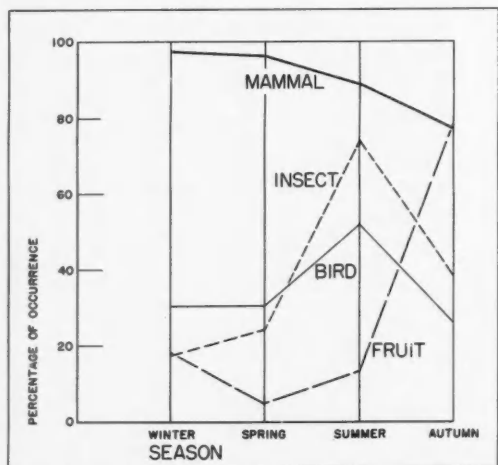


FIG. 12. Seasonal trends of major food groups represented in 2,500 coyote seats collected in Nebraska.

acteristic of the two lesser major food groups—insect and fruit (Figs. 8, 11, and 14). The degree of the coyote's dependence upon or opportunistic utilization of birds, insects, and fruits for food is, indeed,

so variable that both areal and seasonal shifts in the order of the quantitative importance of these three food groups are outstanding characteristics of the predator's basic feeding pattern (Figs. 8, 10, 11, 12, 13, and 14).

The seasonal pattern of the major food groups as represented in 2,500 coyote seats (Fig. 12) shows the frequency of mammalian remains highest in winter and spring, somewhat lower in summer, and lowest in the autumn. Sperry (1940) reported the percentage of volume of mammalian remains in coyote stomachs as being slightly less in summer and autumn than in winter and spring. Scott (1943, 1947) found a comparable seasonal pattern in red fox feeding trends, and suggested that it was probably a response to the "increased seasonal availability" of insects and foods of plant origin. Increased availability of insects in summer and of fruit in the autumn are expected phenological conditions. The pattern depicted in Figure 12 indicates that an increased availability of birds, as well as fruit and insects, especially the latter, probably caused the summer depression in the incidence of mammalian remains.

The most striking seasonal shift is the enormous autumnal increase in the frequency of fruit in coyote droppings, accompanied not only by the lowest seasonal occurrence of mammalian remains but by well-defined declines in the frequencies of remains of birds and insects.

The basic order of food groups (mammal, bird, insect, and fruit) characterizes the spring pattern as derived from all seats studied (Fig. 12). The shifts from spring to summer and from summer to autumn appear to be more pronounced than those of the other two seasonal transitions.

The seasonal alignments are not everywhere the same, i.e., there are areal modifications of the overall

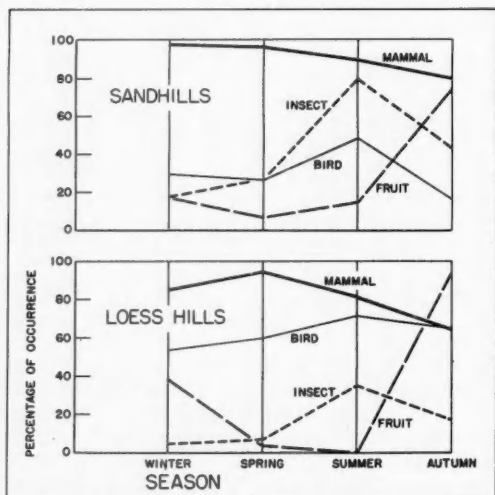


FIG. 13. Seasonal trends of major food groups represented in 2,159 coyote seats collected in sandhills and in 194 seats taken in loess hills.

seasonal pattern. This would be expected upon the basis of areal differences in the basic feeding pattern depicted in Figs. 8, 10, and 11. Each food group, however, shows much the same seasonal trends in the three ecological complexes studied.

There is reason to believe that these seasonal realignments of frequency values are less significant than their graphic expression might suggest. The seasonal percentages of volume presented by Sperry (1941) do not indicate such a pattern. Seasonal differences in relative importance of food groups to the coyote may not occur to a degree comparable to the shifts found in group frequencies in seats. These realignments may, however, point to significant coactions which are implemented through mutual relationships of various food items with the opportunistic coyote. Any specific relationships of that nature are, of course, not revealed by our findings. The significance of even the broad outlines of the seasonal feeding pattern cannot be interpreted with certainty. For example, it has been suggested that increased availability of insects, apparently evidenced by the summer peak of frequency of insect remains in seats, may tend to reduce pressure of coyote predation on the mammalian food group; the graph (Fig. 12) does not indicate that insect increases afford the avian food group a comparable relief from predation pressure by the coyote. On the other hand, it might be conjectured that, in the event insects were for any reason less available, the summer peak of bird remains might climb higher.

### SPECIFIC FEEDING PATTERNS

#### MAMMALS

Twenty-three genera of wild mammals were represented in 747 stomachs and 2,500 seats of coyotes

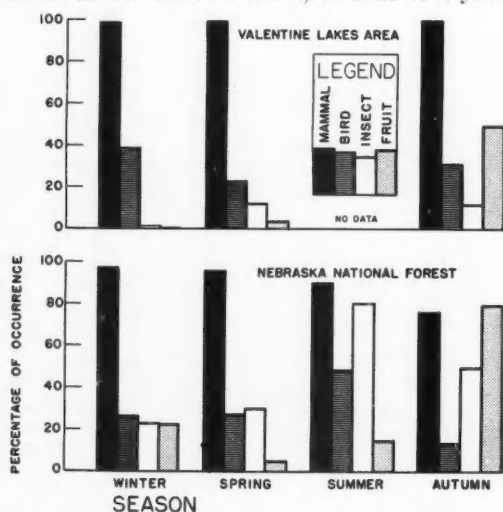


Fig. 14. Seasonal percentages of major food groups in 1,740 coyote seats from a xeric sandhills habitat (Nebraska National Forest) and in 419 seats from an area of lakes and marshes in the sandhills (Valentine Lakes Area).

TABLE 4. Percentages of volume and occurrence of food groups and items in 747 coyote stomachs collected in Nebraska from January 27, 1947 to February 26, 1950, and in 623\* of the 747 stomachs considered susceptible to areal categorization on the basis of land type.

Food groups and items	ALL USABLE STOMACHS 747		ADULT STOMACHS SUSCEPTIBLE TO CATEGORIZATION BY LAND TYPE 623	
	Total contents 170,765 cc		Total contents 148,616 cc	
	% Volume	% Occurrence	% Volume	% Occurrence
MAMMAL.....	78.0	89.3	77.4	89.1
SMALL WILD MAMMAL.....	64.2	83.1	64.7	83.3
Rabbit-mouse-pocket gopher.....	61.8	81.9	62.1	82.3
Rabbit.....	54.0	58.2	55.3	58.9
<i>Sylvilagus</i> .....	36.1	35.7	36.5	37.2
<i>Lepus</i> .....	13.3	12.7	13.8	13.6
Undetermined rabbit.....	4.5	14.5	5.0	13.5
Mouse.....	6.9	39.0	5.8	36.8
<i>Microtus</i> .....	3.2	12.7	2.6	12.0
<i>Reithrodontomys</i> .....	0.9	5.0	0.7	5.0
<i>Peromyscus</i> .....	0.8	5.1	0.8	5.3
<i>Dipodomys</i> .....	0.2	1.5	T	0.2
<i>Perognathus</i> .....	0.1	1.2	0.2	1.1
Other genera <sup>1</sup> .....	0.2	0.9	0.1	0.8
Undetermined mouse.....	1.5	18.6	1.4	18.3
Pocket gopher ( <i>Geomys</i> ).....	0.9	3.5	1.0	3.7
<i>Ondatra</i> .....	1.4	1.6	1.5	1.6
Other genera <sup>2</sup> .....	1.0	2.5	1.1	2.6
DEER.....	0.1	0.4	0.1	0.5
DOMESTIC MAMMAL.....	12.5	26.1	11.4	25.4
Cow.....	8.2	15.7	6.9	13.2
Sheep.....	0.9	0.7	0.7	0.6
Horse.....	0.3	0.1	0.3	0.2
Pig.....	3.2	8.0	3.5	9.5
Undetermined mammal.....	1.2	3.9	1.2	3.7
BIRD.....	17.7	42.8	18.7	41.7
WILD BIRD.....	8.8	26.9	9.6	29.1
Galliformes.....	7.9	16.6	8.9	17.8
Pheasant.....	7.4	14.9	8.4	15.9
Grouse <sup>3</sup> .....	0.4	0.4	0.4	0.5
Undetermined.....	0.2	1.3	0.1	1.4
Duck.....	0.1	0.3	0.1	0.3
Small bird <sup>4</sup> .....	0.3	4.6	0.2	4.5
Undetermined bird.....	0.4	10.8	0.4	9.0
DOMESTIC CHICKEN.....	8.9	14.2	9.1	14.1
REPTILE <sup>5</sup> .....	0.1—	1.1	0.1—	0.8
AMPHIBIAN.....	0.0	0.0	0.0	0.0
FISH.....	0.0	0.0	0.0	0.0
Undetermined vertebrate material.....	1.5	4.6	1.2	4.3
Egg shell.....	T	0.3	T	0.3
INSECT <sup>6</sup> .....	0.9	9.2	0.8	6.4
PLANT MATERIAL.....	1.6	36.1	1.5	33.9
Fruit <sup>7</sup> .....	0.8	3.6	0.7	3.5
Grass.....	0.7	29.0	0.6	26.6
Other.....	0.1	6.0	0.1	5.9
Undetermined material.....	0.1	2.4	0.2	2.2
Nematodes <sup>8</sup> .....	...	44.7	...	45.2
Other non-food material <sup>9</sup> .....	0.2	5.1	0.2	5.1

\*From the 747 usable stomachs, excludes 75 taken in areas of mixed land type, 38 pup stomachs, and 11 stomachs with no data.

<sup>1</sup> *Synaptomys*, *Zapus*, and *Mus*.

<sup>2</sup> *Sorex*, *Blarina*, coyote, *Cynomys*, *Citellus tridecemlineatus*, *Parasciurus*, *Rattus*, and house cat.

<sup>3</sup> Remains in one of the three occurrences identified as pinnated grouse.

<sup>4</sup> Identifiable remains (in three instances only) those of meadowlark and nestling mourning dove.

<sup>5</sup> Snake and lizard.

<sup>6</sup> Dragonfly, grasshoppers, crickets, beetles, and unidentifiable fragments.

<sup>7</sup> Prickly pear cactus, wild plum, wild cherry, Russian olive, and wild grape.

<sup>8</sup> *Physaloptera*.

<sup>9</sup> Sand, soil, rocks, twigs, wood, cloth, cardboard, paper, pieces of rubber hose and boot, an 18-inch length of rope, and wads of coyote hair about sandbars—mostly in stomachs of trapped coyotes.

collected in Nebraska. This number includes one occurrence of skunk not identifiable to genus and excludes coyote, remains of which (mostly hair) were not interpreted as representing a food item. Of these 23 genera, 10 were considered quantitatively important (consistent) enough to warrant tabulation, the others being reported in footnotes to tables.

Identification to species was not routinely undertaken; it can be assumed on the basis of known distributions of mammals in Nebraska, and with reasonable assurance, that 31, and possibly 33 species were represented.

Remains of five kinds of domestic mammals, including house cat, appeared in the materials studied.

It is noteworthy that some mammals that occur generally throughout Nebraska and in all of the three areas of intensive seat collection were not represented in stomachs from all land types nor in seats from all three study areas. These findings suggest significant differences in availability or buffer influences. Also notable are marked discrepancies between apparent availabilities and realized frequencies of occurrence, indicating either undetected availability factors or the operation of predilections on the part of the coyote, or both. These ecological relationships will be considered further in the discussions of specific food items.

The food group "small wild mammal" is arbitrarily segregated in an effort to express the importance of small mammalian prey (jackrabbit and smaller) to the coyote in Nebraska as compared with deer or domestic hoofed mammals. This reliance by coyotes upon small mammals for food is indicated not only by frequency of occurrence in seats (Figs. 15, 16, and 17) but also by percentages of volume in stomachs (Tables 4 and 6). During the period of study and on the basis of 747 stomachs, approximately 65% of the volume of food eaten by coyotes was of small mammal origin. The lowest volume value (50.9%) was shown by stomachs from the sandhills, which also

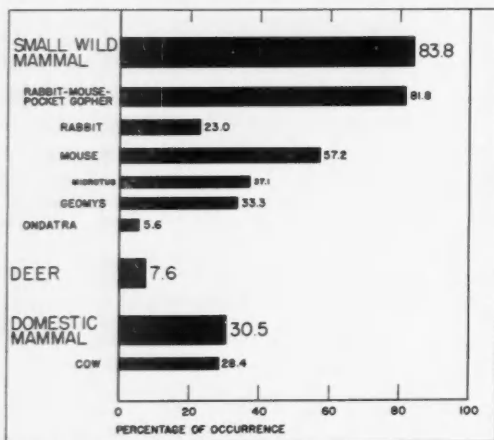


FIG. 15. Percentages of occurrence of certain mammalian food groups and items in 2,500 coyote seats collected in Nebraska.

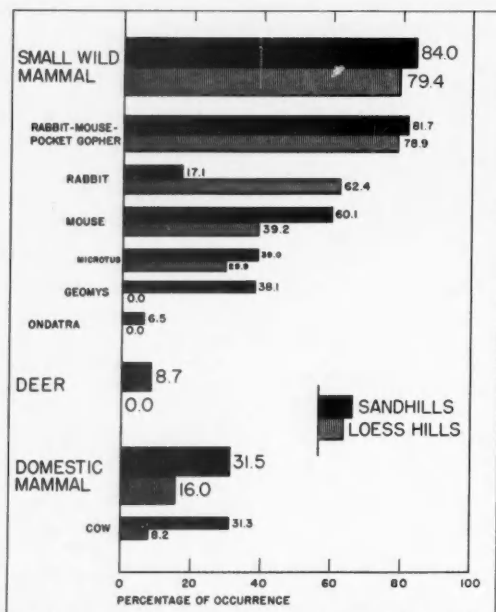


FIG. 16. Percentages of occurrence of certain mammalian food groups and items in 2,159 coyote seats collected in sandhills and in 194 seats taken in loess hills.

yielded the lowest average volume of total contents (Table 1). The highest percentage of volume (86.5%) was found in stomachs from the drift hills.

The seasonal pattern of consumption of small wild mammals (Fig. 19), even in different land types (Fig. 20), is essentially in keeping with the basic seasonal trends of the mammalian food group as a whole (Fig. 12), further emphasizing that the prominence of the latter is in large measure forced by the coyotes' utilization of small wild mammals. Interesting areal modifications in this seasonal pattern can occur, however, as shown by comparison of seasonal occurrence values in seats from the two quite different sandhill areas (Fig. 21). On the Valentine Lakes Area (admitting the weakening absence of data for summer) small wild mammals maintained a year-round frequency at or near 100%, whereas on Nebraska National Forest, where the annual values was less (Fig. 17), seasonal values declined more or less steadily from winter through spring and summer to autumn, with the latter showing an occurrence of 58.8%, a pattern which appears to be a correlative of the summer high of insect remains (80.7%) and the autumnal high of fruit (80.0%).

#### Rabbit-mouse-pocket gopher Group

Of the 23 genera of small wild mammals represented in the coyote seats and stomachs, 11 comprised the "rabbit-mouse-pocket gopher" group and contributed preponderantly to the prominence of the small wild mammal group in the Nebraskan coyotes' feeding



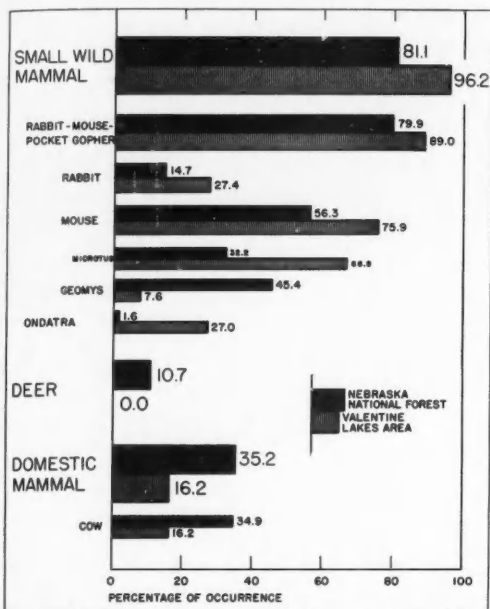


FIG. 17. Percentages of occurrence of certain mammalian food groups and items in 1,740 coyote seats from a xeric sandhills habitat (Nebraska National Forest) and in 419 seats from an area of lakes and marshes in the sandhills (Valentine Lakes Area).

pattern (Figs. 15, 16, 17, and 19), and, indeed, to the dominance of the mammalian food group. That 62% of the total stomach contents examined, or 95% of the volume of small mammal remains, was furnished by rabbits, mice, and pocket gophers also attests their importance as a group. This category is, however, subject to marked areal differences, varying from 33.9% of volume in stomachs from the sandhills to 86.5% in those from drift hills (Table 6).

#### Rabbit

The staple food of first importance in the loess plains, loess hills, and drift hills was rabbit. Treating the four species of lagomorphs that occur in Nebraska as one food item is in keeping with the practice of previous workers (Bond 1939, Sperry 1941) and is done since the rabbit material frequently was not adequate for generic identification. Further justification may exist in that availability of all four species as a function of behavior may conform, more or less, to a family pattern.

The white-tailed jack rabbit (*Lepus townsendii*) occurs in most of Nebraska but in apparently greater abundance in the northern half; the black-tailed jack rabbit (*L. californicus*) is usually present in greater numbers over all but northeastern Nebraska. The eastern cottontail (*Sylvilagus floridanus*) is found throughout the state, while the desert cottontail (*S. auduboni*) occurs only west of about the 100th Meridian, mostly in the high plains. (Common names of mammals after Burt & Grossenheider 1952.)

TABLE 5. Percentages of occurrence of food groups and items in 623 coyote stomachs categorized on the basis of the five major land types in Nebraska, collected from January 27, 1947 to February 26, 1950.

Food groups and items	Number of stomachs				
	32	77	268	153	93
	Western high plains	Sandhills	Loess hills	Loess plains	Drift hills
MAMMAL.....	90.6	96.1	88.8	86.9	87.1
SMALL WILD MAMMAL.....	87.5	89.6	81.0	83.0	83.9
Rabbit-mouse-pocket gopher.....	84.4	85.7	80.2	83.0	83.9
Rabbit.....	40.6	27.3	58.2	69.3	76.3
<i>Sylvilagus</i> .....	28.1	9.1	35.1	43.8	59.1
<i>Lepus</i> .....	0.0	7.8	10.8	28.1	7.5
Undetermined rabbit.....	12.5	13.0	15.3	11.1	12.9
Mouse.....	71.9	62.3	33.6	24.2	33.3
<i>Microtus</i> .....	28.1	24.7	9.7	5.9	12.9
<i>Reithrodontomys</i> .....	9.4	7.8	6.7	2.0	1.1
<i>Peromyscus</i> .....	6.3	6.5	5.6	4.6	4.3
<i>Dipodomys</i> .....	0.0	1.3	0.0	0.0	0.0
<i>Perognathus</i> .....	3.1	2.6	1.1	0.7	0.0
Other genera <sup>1</sup> .....	0.0	0.0	1.1	0.0	2.2
Undetermined mouse.....	25.0	31.2	16.0	15.0	17.2
Pocket gopher ( <i>Geomys</i> ).....	12.5	19.5	0.7	1.3	0.0
<i>Ondatra</i> .....	0.0	13.0	0.0	0.0	0.0
Other genera <sup>2</sup> .....	15.6	3.9	2.2	1.3	0.0
DEER.....	3.1	0.0	0.4	0.7	0.0
DOMESTIC MAMMAL.....	34.4	39.0	23.9	22.2	20.4
Cow.....	28.1	32.5	9.7	7.8	10.7
Sheep.....	3.1	0.0	0.7	0.7	0.0
Horse.....	0.0	1.3	0.0	0.0	0.0
Pig.....	6.3	2.6	10.8	1.1	9.7
Undetermined mammal.....	0.0	7.8	4.9	2.6	0.0
BIRD.....	53.1	28.6	47.0	50.3	19.4
WILD BIRD.....	40.6	28.6	34.0	32.0	6.5
Galliformes.....	21.9	11.7	21.3	23.5	2.2
Pheasant.....	18.8	9.1	19.8	20.9	1.1
Grouse <sup>3</sup> .....	3.1	0.0	0.4	0.7	0.0
Undetermined.....	0.0	2.6	1.1	2.0	1.1
Duck.....	0.0	1.3	0.4	0.0	0.0
Small bird <sup>4</sup> .....	6.3	18.2	3.0	2.6	0.0
Undetermined bird.....	12.5	11.7	10.4	7.2	4.3
DOMESTIC CHICKEN.....	12.5	0.0	14.9	20.9	12.9
REPTILE <sup>5</sup> .....	3.1	5.2	0.0	0.0	0.0
AMPHIBIAN.....	0.0	0.0	0.0	0.0	0.0
FISH.....	0.0	0.0	0.0	0.0	0.0
Undetermined vertebrate material.....	6.3	2.6	4.1	6.5	2.2
Egg shell.....	0.0	0.0	0.7	0.0	0.0
INSECT <sup>6</sup> .....	34.4	24.7	2.6	1.3	1.1
PLANT MATERIAL.....	62.5	45.5	26.9	35.3	32.3
Fruit <sup>7</sup> .....	9.4	9.1	3.7	0.7	1.1
Grass.....	50.0	31.2	19.0	32.0	28.0
Other.....	9.4	7.8	7.1	3.3	4.3
Undetermined material.....	0.0	2.6	3.4	0.7	2.2
Nematodes <sup>8</sup> .....	56.3	40.5	47.4	47.7	35.5
Other non-food material <sup>9</sup> .....	0.0	13.0	4.5	5.2	2.2

<sup>1</sup> *Synaptomys*, *Zapus*, and *Mus*.

<sup>2</sup> *Sorex*, *Blarina*, coyote, *Cynomys*, *Citellus tridecemlineatus*, *Parasciurus*, and house cat.

<sup>3</sup> Remains in one of the three occurrences identified as pinnaed grouse.

<sup>4</sup> Identifiable remains (in three instances only) those of meadowlark and nestling mourning dove.

<sup>5</sup> Snake and lizard.

<sup>6</sup> Dragonfly, grasshoppers, crickets, beetles, and unidentifiable fragments.

<sup>7</sup> Prickly pear cactus, wild plum, wild cherry, and wild grape.

<sup>8</sup> *Physaloptera*.

<sup>9</sup> See footnote 9, Table 4.

That rabbits furnished a preponderance of the coyote's food throughout much of Nebraska is also in keeping with previous findings. Sperry (1941) reported that "rabbits easily took first place in the diet, whether the rating was by volume or by frequency." In 8,263 coyote stomachs from 17 western

and midwestern states, Sperry found rabbits composing 33% of the total volume of food materials and occurring in 43% of the stomachs. Rabbit re-

TABLE 6. Percentages of volume of food groups and items in 623 coyote stomachs categorized on the basis of the five major land types in Nebraska, collected from January 27, 1947 to February 26, 1950. For footnotes, see below Table 5.

Food groups and items	Total volume of stomach contents				
	6755 cc	14,686 cc	60,371 cc	42,545 cc	24,259 cc
	Western High plains	Sandhills	Loess hills	Loess plains	Drift hills
MAMMALS.....	72.6	76.6	78.7	67.9	92.4
SMALL WILD MAMMAL.....	59.6	50.9	62.3	61.2	86.5
Rabbit-mouse-pocket gopher.....	57.3	33.9	60.6	60.9	86.5
Rabbit.....	36.8	12.7	55.2	57.9	82.2
<i>Sylvilagus</i> .....	35.9	7.3	35.7	27.9	71.4
<i>Lepus</i> .....	0.0	3.9	12.0	26.6	5.5
Undetermined rabbit.....	0.9	1.5	7.5	3.2	5.3
Mouse.....	17.3	13.8	5.3	2.9	4.2
<i>Microtus</i> .....	10.9	7.0	1.7	1.3	2.1
<i>Reithrodontomys</i> .....	1.2	2.8	0.8	0.3	0.1
<i>Peromyscus</i> .....	1.0	1.5	1.0	0.3	0.8
<i>Dipodomys</i> .....	0.0	0.1	0.0	0.0	0.0
<i>Perognathus</i> .....	0.5	0.8	0.1	0.1	0.0
Other genera <sup>1</sup> .....	0.0	0.0	0.2	0.0	0.2
Undetermined mouse.....	3.8	1.6	1.5	1.0	1.1
Pocket gopher ( <i>Geomys</i> ).....	3.2	7.4	0.2	0.1	0.0
<i>Onychomys</i> .....	0.0	14.7	0.0	0.0	0.0
Other genera <sup>2</sup> .....	2.3	2.3	1.7	0.3	0.0
DEER.....	0.1	0.0	0.1	T	0.0
DOMESTIC MAMMALS.....	12.9	20.4	14.7	6.6	6.0
Cow.....	12.3	17.0	7.9	3.0	3.3
Sheep.....	0.5	0.0	1.6	0.1	0.0
Horse.....	0.0	3.4	0.0	0.0	0.0
Pig.....	T	T	5.2	3.5	2.7
Undetermined mammal.....	0.0	5.3	1.6	T	0.0
BIRD.....	20.3	8.3	18.3	29.3	7.3
WILD BIRD.....	12.1	8.3	12.0	11.4	0.6
Galliformes.....	11.6	7.5	11.0	11.0	T
Pheasant.....	3.1	7.1	10.9	10.8	T
Grouse <sup>3</sup> .....	8.4	0.0	0.1	0.1	0.0
Undetermined.....	0.0	0.4	0.1	0.1	T
Duck.....	0.0	0.1	0.3	0.0	0.0
Small bird <sup>4</sup> .....	0.1	0.1	0.2	0.3	0.0
Undetermined bird.....	0.4	0.5	0.5	0.1	0.6
DOMESTIC CHICKEN.....	8.2	0.0	6.2	17.9	6.7
REPTILE <sup>5</sup> .....	0.1	0.2	0.0	0.0	0.0
AMF.....	0.0	0.0	0.0	0.0	0.0
FI <sup>6</sup> .....	0.0	0.0	0.0	0.0	0.0
Utebrate material.....	0.9	1.1	1.0	2.3	0.1
Egg.....	0.0	0.0	T	0.0	0.0
INSECT <sup>6</sup> .....	3.3	6.7	0.1	0.1	T
PLANT MATERIAL.....	2.5	5.3	1.8	0.2	0.2
Fruit <sup>7</sup> .....	1.4	1.7	1.3	T	T
Grass.....	0.9	3.6	0.5	0.1	0.2
Other.....	0.2	0.1	T	0.1	1.0
Undetermined material.....	0.0	1.1	0.1	T	0.1
Non-food material <sup>8</sup> .....	0.3	0.8	0.1	0.2	0.1

mains occurred in 58% of 747 stomachs from Nebraska and constituted 54% of the total volume of contents (Table 4), comprising thereby 70% of the total volume of mammalian remains.

The occurrence of rabbit remains in the 2,500 seats (23%) is somewhat less convincing (Fig. 15). It must be remembered, however, that most of the seats (74% of the 2,353 collected on study areas) were taken in the Bessey Division of Nebraska National Forest where rabbit populations were known to be very low. The overall data furnished by seats therefore strongly reflect conditions in that situation. The significance of that explanation appears in a comparison of frequency values of rabbit remains in seats from sandhills and loess hills (Fig. 16). The occurrence of rabbit remains in 62.4% of the seats from loess hills reflects the known, albeit unmeasured abundance of rabbits in that land type. These areal differences are likewise depicted in Figure 18, which also serves to illustrate (1) the preponderant bulk of rabbit in stomachs from loess hills and plains and drift hills, and (2) the parallel values of occurrence and volume shown by this food.

Rabbit remains in stomachs from the loess plains were about equally composed of jack rabbit and cottontail, about three-fourths cottontail in stomachs from loess hills, and approximately 90% cottontail in those from drift hills. In 200 mi of driving in the summer of 1948 (sunrise to one hour after sunrise over 20 mi counting routes established for the experimental phase of this study) in loess plains (Clay, Fillmore, and Thayer counties), Mr. Bernard

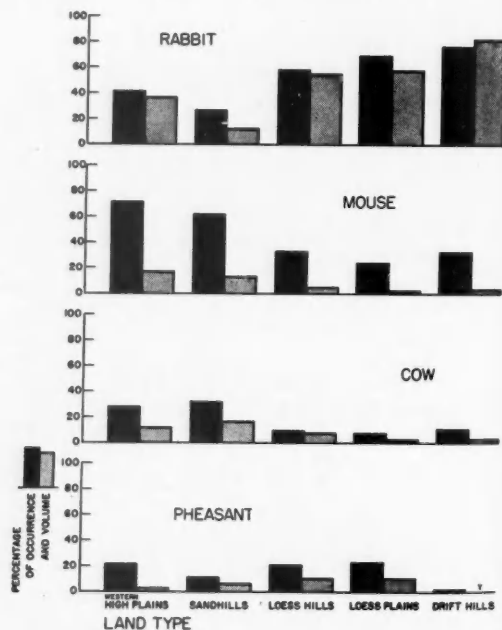


FIG. 18. Percentages of occurrence and volume of remains of rabbit, mouse, cow, and pheasant in 623 coyote stomachs from five land types in Nebraska.

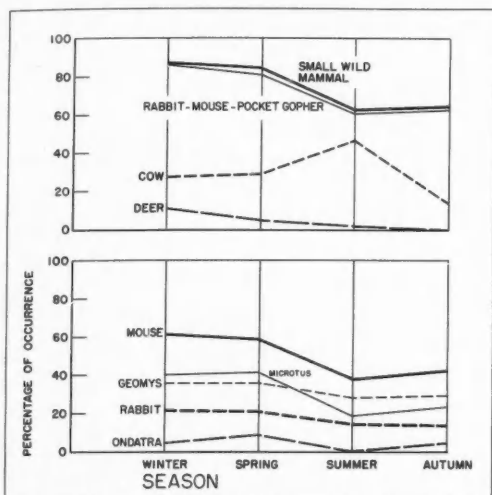


FIG. 19. Seasonal trends of certain mammalian food groups and items represented in 2,500 coyote seats collected in Nebraska.

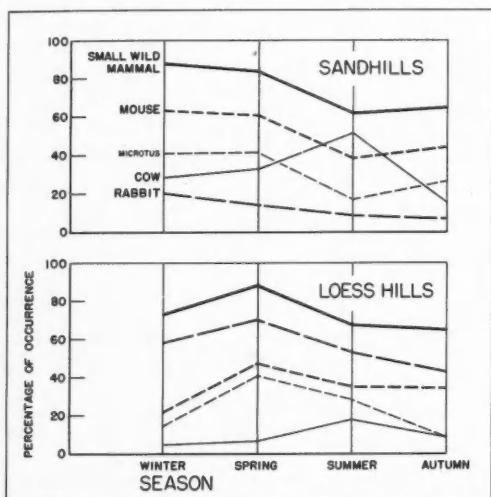


FIG. 20. Seasonal trends of certain mammalian food groups and items represented in 2,159 coyote seats collected in sandhills and in 194 seats taken in loess hills.

Leman recorded 32 cottontails per 100 mi; in 80 mi of driving in loess hills (Valley County) he saw 45 cottontails per 100 mi, and in 300 mi of driving in drift hills (Pawnee and Richardson counties), 71 cottontails per 100 mi. The function of availability by virtue of population densities is strongly suggested here.

Seasonal utilization of rabbit as determined here showed strikingly different local patterns. Only in the loess hills did the seasonal pattern (Fig. 20) with its spring peak tend to conform to that depicted by Sperry (1941), who reported "the average percentage of rabbits consumed for March, April, and May"

somewhat "above the average for the year." In the Valentine Lakes Area, where this food item apparently ranked second in the coyotes' diet (Fig. 17), frequency of rabbit was much higher in winter than in spring (Fig. 22). Sather found evidence that coyotes were concentrating on cottontails in Ballard's Marsh during "the big blizzard" of January, 1949, the rabbits apparently being caught in holes in the very large drifts. On the Nebraska National Forest (Fig. 22) the seasonal pattern of rabbit utilization tended "from a winter high gradually downward to a fall low" as described by Scott (1943) for red fox. Inasmuch as three-fourths of the seats used in determining seasonal patterns were gathered on the National Forest, the trend there largely determined the general pattern depicted in Figure 19 and that for sandhills in Figure 20. Reasons for the nonconformities in seasonal trends are not apparent.

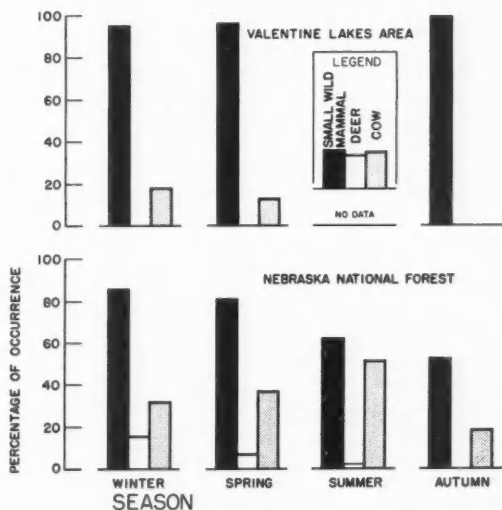


FIG. 21. Seasonal percentages of occurrence in 1,740 coyote seats from a xeric sandhills habitat (Nebraska National Forest) and in 419 seats from an area of lakes and marshes in the sandhills (Valentine Lakes Area).

The dependence of coyotes on rabbits with its marked trend upward in spring, when both rabbit and game birds are producing young, may be significant in assaying both the coyote and the rabbit in the total wildlife and land management picture.

In that connection, the following information may be of interest. The number of coyotes on the Bessey Division in 1949 was estimated by Forest Service personnel to be 450. Thereafter numerical estimates were discontinued in favor of generalized statements of trends. Reports on the coyote population on the 90,000 ac reserve since 1949 read as follows: 1950 "common, increasing"; 1951 "common, stationary"; 1952 "occasional, decreasing"; 1953 "rare, decreasing." Mr. Noble E. Buell, District Agent, Branch of Predator and Rodent Control of the Fish and Wildlife Service, has informed us that

"1080" stations for the decimation of coyotes numbered 42 in Blaine and Thomas counties in the winter of 1951-52, 35 in the winter of 1952-53. In a recent (November 17, 1953) communication, Mr. Ralph R. Hill of the U. S. Forest Service states: "Earlier this year I spent parts of two days in the field on the Bessey Division without seeing a coyote track or fresh sign. The contrast with conditions ten years ago is remarkable. I cannot recall seeing cottontails ten years ago, except along the river bottoms. Jack rabbits were seen occasionally back in the sandhills. Cottontails are now numerous in the older cedar plantations. They have been feeding on the accessible bark of the lower side-limbs. Whether they will work on the main trunks when the side-branches are girdled remains to be seen. I anticipate that rabbit 'problems' will develop." Mr. Hill explains that his observations do not "necessarily imply that coyotes are a factor in cottontail abundance," and points out the development of excellent cover for cottontails in the cedar plantations as another variable. Be that as it may, the need for deeper inquiry into compensatory functions of the biotic community is abundantly clear.

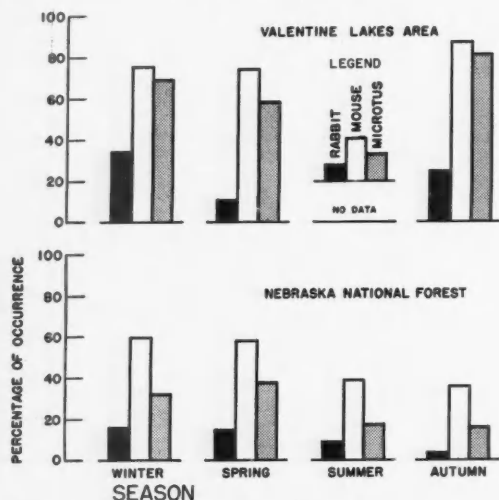


FIG. 22. Seasonal percentages of occurrence of remains of rabbit, mouse, and meadow mouse (*Microtus*) in 1,740 coyote seats from a xeric sandhills habitat (Nebraska National Forest) and in 419 seats from an area of lakes and marshes in the sandhills (Valentine Lakes Area).

### Mice

Mice were eaten often by coyotes (Figs. 15 and 18) but contributed rather meagerly to the total volume of food (Fig. 18). While remains of mice were found in 39% of all stomachs examined, only 6.9% of the volume of food materials present was composed of mouse (Table 4).

Mice were apparently much more important to coyotes in the high plains and sandhills than in the loess and glacial drift land types (Fig. 18). Com-

parison of the values furnished by remains of mice and rabbits in stomachs suggests that where rabbits are less abundant the coyote relies more heavily upon mice. That the contents of stomachs from the high plains and sandhills showed an average volume 20% less than that of stomachs from the other three land types (Table 1) suggests that where dependence upon the smallest prey species is greater, the coyote gets along on somewhat less food.

Frequency of mouse remains in coyote seats showed the same areal differences (Fig. 16). Comparison of these values in the two sandhills areas indicates that mice were considerably more important in the coyotes' diet in the more moist situation.

Seasonal trends in the incidence of mouse remains in seats, which strongly influence the seasonal patterns of both the small wild mammal group and the mammalian food group as a whole, show a winter-spring high followed by a summer-fall depression in Nebraska National Forest (Fig. 21), a marked spring peak in the loess hills with winter and autumnal lows (Fig. 20), and a distinct autumnal high in the Valentine Lakes Area (Fig. 22). These varying patterns are considerably influenced by *Microtus*, and are discussed further in the section concerning that genus.

The Heteromyidae and Cricetidae furnished nearly all of the mammalian remains categorized as mouse. *Perognathus* and *Dipodomys* were relatively unimportant. Of the cricetid genera, *Reithrodontomys*, *Peromyscus*, and *Microtus*, the latter emerged as one of the four principal mammalian food items; patterns of utilization of *Microtus* by coyotes largely dictate those of the mouse group as a whole.

**Meadow Mice.** Three species of meadow mice occur in Nebraska, the meadow vole (*Microtus pennsylvanicus*), the prairie vole (*M. ochrogaster*), and the pine vole (*M. pinetorum*). The meadow vole is found over most of the state and is especially abundant in marshy lands and wet meadows. The prairie vole is common throughout the entire state in grasslands, borders of cultivated fields and under shrubby cover, and is not uncommon in damp situations. The pine vole in Nebraska is confined to the drift hills. The three species are treated as one food item because specific identification of remains was not routinely practiced. The close conformity of the habits of the three species alone justifies this practice.

Meadow mice were generally eaten in greater numbers than was any other generically determined mouse, and with a frequency that would indicate that they provide a staple food supply for the coyote (Figs. 15 and 17). The frequency of their remains surpassed that of rabbit in some situations. Measurements afforded by the 747 stomachs indicate, however, that *Microtus* generally contributed only 3.2% of the total volume of food albeit about one-half of the total volume of mouse (Table 4).

Substantial areal differences in both frequency and volume values (Figs. 17 and 23 and Tables 5 and 6) indicate that *Microtus* is not relied upon by the coyote equally in all environmental complexes. Admitting



TABLE 7. Percentages of occurrence of food groups and items in 2500 coyote seats collected in Nebraska from February 26, 1947 to March 20, 1951.

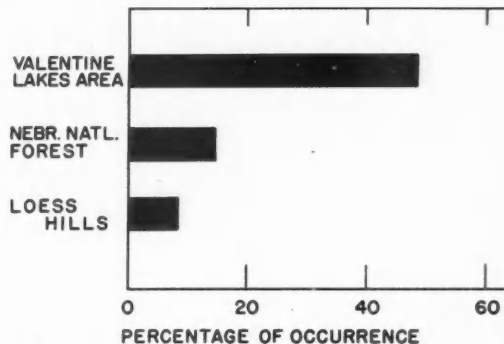
Food groups and items	Number of seats	IN ALL SEATS	IN SEATS FROM STUDY AREAS*					
		2500	1230	800	204	119	2353	
		All seasons	Winter	Spring	Summer	Autumn	All	
MAMMAL.....		95.1	97.6	96.5	89.2	77.3	95.5	
SMALL WILD MAMMAL.....		83.8	88.0	84.9	63.2	65.5	83.6	
Rabbit-mouse-pocket gopher.....		81.8	86.8	81.3	60.8	63.0	81.5	
Rabbit.....		23.0	22.0	21.6	15.2	14.3	20.9	
Sylvilagus.....		5.7	5.7	6.5	1.5	0.8	5.4	
Lepus.....		5.0	5.4	5.3	3.9	2.5	5.1	
Undetermined rabbit.....		12.3	10.9	10.1	9.8	10.9	10.5	
Mouse.....		57.2	62.3	59.6	38.7	42.9	58.5	
Microtus.....		37.1	40.5	41.8	19.1	23.5	38.2	
Reithrodontomys.....		8.9	12.7	6.0	2.9	8.4	9.3	
Peromyscus.....		1.4	0.9	1.8	2.0	1.7	1.3	
Dipodomys.....		4.8	5.7	4.1	2.0	4.2	4.8	
Perognathus.....		3.7	2.5	4.6	6.9	8.4	3.9	
Other genera.....		0.0	0.0	0.0	0.0	0.0	0.0	
Undetermined mouse.....		14.0	15.0	13.1	13.2	12.6	14.1	
Pocket gopher ( <i>Geomys</i> ).....		33.3	36.1	36.1	28.4	26.1	34.9	
Ondatra.....		5.6	5.1	8.9	0.5	5.0	6.0	
Other genera <sup>1</sup> .....		3.2	3.1	2.8	7.8	1.7	3.3	
DEER.....		7.6	11.5	5.1	2.0	0.0	7.9	
DOMESTIC MAMMAL.....		30.5	28.9	29.9	48.0	15.1	30.2	
Cow.....		28.4	27.9	29.5	47.0	14.3	29.4	
Sheep.....		0.0	0.0	0.0	0.0	0.0	0.0	
Horse.....		0.3	0.3	0.0	0.0	0.0	0.2	
Pig.....		0.8	0.7	0.4	1.5	0.8	0.7	
Undetermined mammal.....		6.2	4.5	5.0	18.6	13.4	6.3	
BIRD.....		33.5	30.3	30.4	52.0	26.1	32.0	
WILD BIRD.....		32.6	30.3	30.1	50.5	24.4	31.7	
Galliformes.....		15.9	15.9	14.9	14.7	12.6	15.3	
Pheasant.....		6.4	5.7	5.9	5.9	4.2	5.7	
Grouse <sup>2</sup> .....		4.7	6.3	3.8	3.4	1.7	5.0	
Undetermined.....		5.0	4.0	5.5	5.4	6.7	4.8	
Duck.....		1.2	1.8	0.6	0.0	0.0	1.1	
Small bird <sup>3</sup> .....		4.5	2.0	4.1	21.1	3.4	4.5	
Undetermined.....		11.6	11.3	10.9	16.2	8.4	11.4	
DOMESTIC CHICKEN.....		1.1	0.0	0.4	2.9	1.7	0.5	
REPTILE <sup>4</sup> .....		5.4	3.3	7.4	13.7	2.5	5.5	
AMPHIBIAN <sup>5</sup> .....		0.1	0.0	0.1	0.0	0.0	0.1	
FISH.....		0.1	0.0	0.4	0.0	0.0	0.1	
Undetermined vertebrate material.....		1.0	0.8	1.0	1.0	1.7	0.9	
Egg shell.....		3.6	1.0	5.0	11.3	0.8	3.2	
INSECT <sup>6</sup> .....		26.0	17.6	24.6	74.5	38.7	26.0	
PLANT MATERIAL.....		39.2	34.6	33.5	56.9	84.0	38.6	
Fruit <sup>7</sup> .....		16.0	18.4	4.9	13.2	79.0	16.4	
Grass.....		24.4	18.1	26.1	47.5	23.5	23.7	
Other.....		4.1	4.1	3.8	4.4	4.2	4.0	
Undetermined material.....		0.2	0.2	0.3	0.0	0.0	0.2	

\* Excluding 58 known coyote pup seats collected at den sites in study areas.

<sup>1</sup> See footnote 1 below Table 8.<sup>2</sup> See footnote 2 below Table 8.<sup>3</sup> See footnote 3 below Table 8.<sup>4</sup> Largely lizard; remains of snake also represented.<sup>5</sup> Frog.<sup>6</sup> See footnote 7 below Table 8.<sup>7</sup> See footnote 8 below Table 8.

the probable inaccuracies occasioned by the presence of mouse remains the generic identities of which were not determined, our data indicates (Table 5) that meadow mice were fed upon most frequently (28.1%) in the high plains and here contributed their highest percentage (10.9%) to the volume of food. These mice appear to have been least important in the coyote's diet in the loess plains, their remains occurring in 5.9% of the stomachs and forming only 1.3% of the volume of contents. Their status as a food item was about the same in the loess hills and drift hills where it was slightly more important than in the plains. In the sandhills, consumption values closely approached those of the high plains. That coyotes in sandhills ate more *Microtus* than those in loess hills is also indicated by frequencies of occurrence in seats (Fig. 16).

The markedly different percentages of occurrence in seats from the two sandhills areas (Fig. 17) is of special interest. *Microtus* remains were found in 66.8% of the seats gathered on the Valentine Lakes area and in slightly less than one-half that many in those from Nebraska National Forest. Although mouse populations were nowhere measured, it is reasonably certain on the basis of field experience that *Microtus* was much more abundant on the Valentine Lakes Area where wet meadows and marshy areas provide extensive habitat for this genus and especially for *M. pennsylvanicus*. Sather observed coyotes pouncing, a hunting method described by Murie (1940) as the "mousing behavior" (see Murie 1945) in heavy stands of river bulrush (*Scirpus fluviatilis*) and sedge (*Carex lacustris*) where meadow mice were known to be abundant. The high frequency of unit seats containing remains of more than one (up to six) meadow mice was early apparent in our examination of seats from the Valentine Lakes area. A comparison of the percentages of occurrence of such seats from the three collection areas (Fig. 23), plus the fact that the volume of *Microtus* virtually equalled that of cottontail in sandhills stomachs, emphasizes the importance of this food

FIG. 23. Percentages of occurrence of coyote seats containing remains of more than one individual of *Microtus*, based upon the number of seats containing remains of such.

source to coyotes in the lake and marsh area of the sandhills.

Sperry (1941) determined that "meadow mice were most frequent in the winter stomachs of coyotes (11%) and occurred least often (4%) in those collected in spring," and concluded that "even in periods of normal reproduction, a fall-winter population peak is indicated for *Microtus*" in keeping with previously published information on population rhythms in mice. Murie (1936) and Scott (1943) have shown that occurrences of meadow mice in red fox seats are more frequent during the cold months, declining as warm weather approaches. Murie (1940) reported that during winter months meadow mice "represent a minor item in the diet" of the coyote in portions of the Yellowstone where, because of deep snows, other foods are more available and where, from April to November, *Microtus*, along with pocket gopher, "is the staple food item."

The unusually deep snows of the winter of 1948-49 (described in the section on deer) apparently lessened the pressure of coyote predation on *Microtus* in Nebraska National Forest (Fig. 25). This depression may also be reflected in the winter low evident in the seasonal pattern of meadow mouse remains in seats from both the Forest Reserve and the loess hills study areas, based on lumped seasonal values (Figs. 20 and 22). On the other hand, a winter low is not shown in the material from the Valentine Lakes area. Remains of *Microtus* were found in 40.0% of 40 stomachs collected in sandhills in winter, in only 8.1% of 37 stomachs taken throughout the other seasons in the same land type. Reasons for these differences are not apparent.

It is perhaps significant that the seasonal trend in the Valentine Lakes area, where meadow mice were abundant and heavily preyed upon by coyotes, appears to conform with the pattern described by Sperry (1941). The autumnal high of 81.3% frequency in this sandhill marsh area is outstanding.

*Other mice.* The harvest mouse (*Reithrodontomys*), of which two species are found in Nebraska, was apparently much less important than *Microtus* in the coyote's diet, and was utilized most frequently in winter and in the high plains and sandhills. Its highest seasonal frequency occurred in winter seats on Nebraska National Forest. A notable feature in this situation was the rather frequent occurrence of seats with remains of several (up to ten) individuals of *Reithrodontomys* per unit seat. The deer mouse (*Peromyscus maniculatus*) and the white-footed mouse (*P. leucopus*), remains of which were identified only to genus, contributed much less to the coyote's fare than would be expected, considering the almost universal occurrence of the genus. Comparable low frequencies have been reported elsewhere as characterizing coyote-*Peromyscus* relationships. The relatively light coyote pressure on *Peromyscus* is probably a function of low availability by virtue of a life habit, i.e., nocturnalism, which exerts a greater ecological influence in this respect than that exerted

by numbers. With remains occurring only in those stomachs and seats from the sandhills where it abounds, the kangaroo rat (*Dipodomys ordi*) was infrequently eaten by coyotes during the period of our study. These nocturnal rodents, whose burrows and trails evidenced their abundance, were very commonly seen along the road when we drove in Nebraska National Forest after dark, and everywhere else in the sandhills. They can be caught by hand if the beam from a flashlight is kept on them. A seemingly high availability as a function of numbers is, however, not realized in the coyote's feeding pattern. This might suggest that the kangaroo rat is not preferred by the coyote. It seems more probable that the period of its activity above the ground plus its escape behavior renders it less available than other prey to the coyote which, like any predator, will, within limits, eat what it can get most easily.

Pocket mice of the genus *Perognathus*, with four species present in Nebraska, were represented in stomachs from all land types excepting drift hills, more frequently in the west and north, and are probably most noteworthy for a steadily ascending percentage of occurrence in sandhill seats from a winter low of 2.6% to an autumnal high of 10.4%.

#### Pocket Gopher

The pocket gopher is of special interest because of its marked importance in the feeding patterns of coyotes in the sandhills.

Two genera of pocket gophers occur in Nebraska, *Thomomys* in the western high plains and *Geomys* throughout the entire state. No remains of *Thomomys* were found in the coyote stomachs and droppings examined. Although two species of *Geomys* inhabit Nebraskan soils, no attempt was made to identify pocket gopher remains further than the genus which is treated here as one food item.

Pocket gopher was represented in stomachs from all land types excepting drift hills, but its frequency in stomachs from the loess types was so low as to make it appear to have been of little importance to the coyote in those areas. On the other hand, its remains appeared in 12.5% of the stomachs from the high plains and in 19.5% of those from the sandhills in which its volume (7.4%) slightly exceeded that of *Microtus*. Remains of pocket gopher in seats from the study areas present an even more striking contrast, occurring in 38.1% of the sandhills seats, in none of those from loess hills (Fig. 16). This rodent's importance to the coyote was also widely variant in the two sandhill situations (Fig. 17), being represented in 7.6% of the seats from the Valentine Lakes area, and in 45.4% of those collected in the Bessey Division of Nebraska National Forest.

*Geomys* occurs in both loess hills and sandhills. Unfortunately, no measurements of populations were made, but pocket gophers are known to be common in loess soils, being abundant in alfalfa fields in and about the study areas on that land type. Aerial observations by Fichter over many miles of both land types gave the impression that pocket gophers were

TABLE 8. Seasonal and areal percentages of occurrence of food groups and items in 2353 coyote seats collected in sandhills and loess hills study areas in Nebraska from February 26, 1947 to March 20, 1951.

Food groups and items	STUDY AREAS									
	SANDHILLS					LOESS HILLS				
	1189	698	176	96	2159	41	102	28	23	194
	Winter	Spring	Summer	Autumn	All	Winter	Spring	Summer	Autumn	All
MAMMAL.....	98.0	96.7	90.3	80.2	96.2	85.4	95.1	82.1	65.2	87.6
SMALL WILD MAMMAL.....	88.5	84.4	62.5	65.6	84.0	73.2	88.2	67.9	65.2	79.4
Rabbit-mouse-pocket gopher.....	87.3	80.2	60.2	62.5	81.7	73.2	88.2	64.3	65.2	78.9
Rabbit.....	20.7	14.5	9.1	7.3	17.1	58.5	70.6	53.6	43.5	62.4
<i>Sylvilagus</i> .....	5.0	2.4	0.6	0.0	3.6	26.8	34.3	7.1	4.3	25.3
<i>Lepus</i> .....	5.5	3.2	2.3	2.1	4.3	2.4	19.6	14.3	4.3	13.4
Undetermined rabbit.....	10.3	8.9	6.3	5.2	9.3	29.3	18.6	32.1	34.8	24.7
Mouse.....	63.7	61.3	39.2	44.8	60.1	22.0	48.0	35.7	34.8	39.2
<i>Microtus</i> .....	41.4	41.8	17.6	27.1	39.0	14.6	41.2	28.6	8.7	29.9
<i>Reithrodontomys</i> .....	13.0	5.7	3.4	8.3	9.7	2.4	7.8	0.0	8.7	5.7
<i>Peromyscus</i> .....	0.9	1.4	0.6	1.0	1.1	0.0	3.9	10.7	4.3	4.1
<i>Dipodomys</i> .....	5.9	4.7	2.3	5.2	5.2	0.0	0.0	0.0	0.0	0.0
<i>Perognathus</i> .....	2.6	5.2	8.0	10.4	4.2	0.0	1.0	0.0	0.0	0.5
Other genera.....	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Undetermined mouse.....	15.3	13.9	15.3	12.5	14.7	4.9	7.8	0.0	13.0	6.7
Pocket gopher ( <i>Geomys</i> ).....	37.3	41.4	33.0	32.3	38.1	0.0	0.0	0.0	0.0	0.0
<i>Ondatra</i> .....	5.3	10.2	0.6	6.3	6.5	0.0	0.0	0.0	0.0	0.0
Other genera <sup>1</sup> .....	3.2	2.9	8.5	2.1	3.5	0.0	2.0	3.6	0.0	1.5
DEER.....	11.9	5.9	2.3	0.0	8.7	0.0	0.0	0.0	0.0	0.0
DOMESTIC MAMMAL.....	29.0	32.8	51.7	15.6	31.5	26.8	9.8	25.0	13.0	16.0
Cow.....	28.7	32.8	51.7	15.6	31.3	4.9	6.9	17.9	8.7	8.2
Sheep.....	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Horse.....	0.3	0.0	0.0	0.0	0.1	2.4	0.0	0.0	0.0	0.5
Pig.....	0.1	0.0	0.0	0.0	0.1	19.5	2.9	10.7	4.3	7.7
Undetermined mammal.....	4.2	4.9	20.5	15.6	6.3	12.2	5.9	7.1	4.3	7.2
BIRD.....	29.5	26.6	48.9	16.7	29.6	53.7	55.9	71.4	65.2	58.8
WILD BIRD.....	29.5	26.6	48.9	16.7	29.6	53.7	53.9	60.7	56.5	55.2
Galliformes.....	15.0	11.6	9.7	6.3	13.1	41.5	37.2	46.4	39.1	39.7
Pheasant.....	4.6	2.6	2.3	0.0	3.6	36.6	28.4	28.6	21.7	29.4
Grouse <sup>2</sup> .....	6.6	4.3	4.0	2.1	5.4	0.0	0.0	0.0	0.0	0.0
Undetermined.....	4.0	5.0	3.4	4.2	4.3	4.9	8.8	17.9	17.4	10.3
Duck.....	1.9	0.7	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0
Small bird <sup>3</sup> .....	2.0	4.2	22.7	4.2	4.5	2.4	3.9	10.7	0.0	4.1
Undetermined.....	11.4	10.5	17.0	6.3	11.3	9.8	13.7	10.7	17.4	12.9
DOMESTIC CHICKEN.....	0.0	0.0	0.0	0.0	0.0	0.0	2.9	21.4	8.7	5.7
REPTILE <sup>4</sup> .....	3.3	8.3	15.9	2.1	5.9	2.4	1.0	0.0	4.3	1.5
AMPHIBIAN <sup>5</sup> .....	0.0	0.1	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0
FISH.....	0.0	0.4	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0
Undetermined vertebrate material.....	0.8	1.1	1.1	1.0	1.0	0.0	0.0	0.0	4.3	0.5
Egg shell <sup>6</sup> .....	0.9	3.7	8.0	0.0	2.4	2.4	13.7	32.1	4.3	12.9
INSECT <sup>7</sup> .....	18.0	27.2	80.7	43.8	27.2	4.9	6.9	35.7	17.4	11.9
PLANT MATERIAL.....	34.2	33.0	56.8	80.2	37.7	43.9	37.3	57.1	100.0	49.0
Fruit <sup>8</sup> .....	17.7	5.0	15.3	75.0	15.9	39.0	3.9	0.0	95.6	21.6
Grass.....	17.7	25.8	47.2	17.7	22.7	29.3	28.4	50.0	47.8	34.0
Other <sup>9</sup> .....	3.9	3.4	2.8	3.1	3.6	9.8	5.9	14.3	8.7	8.2
Undetermined material.....	0.2	0.3	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0
Non-food material <sup>10</sup> .....	1.1	2.6	0.6	0.0	1.5	2.4	3.9	0.0	4.3	3.1

<sup>1</sup> In sandhills: *Scalopus*, *Sorex*, undetermined shrew, *Mustela frenata*, *Mustela vison*, undetermined skunk, coyote, *Citellus*, *Cynomys*, *Parasciurus*, and *Erethizon*; in loess hills: *Citellus*, *Cynomys*, *Perognathus hispidus*, and *Rattus*.

<sup>2</sup> Probably sharp-tailed grouse only.

<sup>3</sup> In sandhills: Mourning dove and meadowlark, plus undetermined small birds; for convenience, includes heron and coot. All small bird remains in seats from loess hills undetermined.

<sup>4</sup> Largely lizard.

<sup>5</sup> Frog.

<sup>6</sup> Includes shell of reptile eggs in sandhills.

<sup>7</sup> Orthoptera, Coleoptera, and undetermined larvae (not dermestid).

<sup>8</sup> In sandhills: Hackberry, sand cherry, choke cherry, wild plum, and wild grape. In loess hills: Wild plum.

<sup>9</sup> Includes corn.

<sup>10</sup> Largely sand or soil; includes paper, clam shell, lead shot, and rubber.

somewhat more abundant in the sandhills, if number of mounds can be relied upon even as a loose indicator of population densities. Even a known differential of considerable magnitude in populations of the prey species would not, however, seem to account for the striking discrepancy in frequencies of remains in coyote stomachs and seats in the two land types. Pocket gophers were available to coyotes in both situations, insofar as numbers were concerned, although perhaps not equally so.

Three factors that might account for these areal differences are observable:

(1) The pocket gophers in the loess hills study areas and those in Nebraska National Forest differ subspecifically and might, therefore, exhibit significantly different habits.

(2) The relatively high availability of rabbits by virtue of numbers may have served to buffer coyote pressure on the pocket gopher in the loess hills. The complete absence of gopher remains in stomachs from drift hills where cottontail populations were highest might further suggest this possibility.

(3) Sandy soils increase the pocket gopher's vulnerability to predation by coyotes.

All three of these factors, and even more, may operate simultaneously, of course. The last, however, is most susceptible to analysis here.

It might at first seem that pocket gophers are more available in the loose soils of the sandhill region than in loess soils—if coyotes secure gophers by digging—not only because of differences in soil texture, but because burrows of sandhill gophers are usually nearer the surface. However, no evidence that would indicate coyotes had dug out pocket gophers, or even attempted to, was ever observed in Nebraska National Forest. According to Murie (1940), coyotes in Yellowstone Park capture *Thomomys* by waiting at tunnel entrances when the gophers are digging or leaving the burrow to forage. Coyotes were never observed capturing pocket gophers in our study areas, but gophers were commonly seen pushing fresh diggings from open burrows in the very early morning, especially during the spring, in Nebraska National Forest. It can be imagined that the pounce of a coyote, with the forelegs held straight (Murie 1940) and the forefeet coming down on or just behind a pocket gopher in the second or two that it is exposed at the burrow entrance, would frequently cause the sandy soil to cave in behind the rodent and insure its capture. Loess soils would be much less likely to collapse in this manner. The shallower burrows in the sandy soils approach the surface at a considerably sharper angle than is found in the deeper burrow systems of gophers in loess soils, a pattern which would contribute to the vulnerability of the pocket gopher and the coyote's success in catching the rodent at the entrance of its tunnel. Availability may, thereby, be in part a function of soil, especially if the depth of burrows is a function of soil.

Possible causes of the differences in the coyotes' degree of utilization of pocket gophers in the two

sandhill areas must be sought elsewhere than in soil texture, inasmuch as the dune sand of the two situations is the same, or essentially so as a factor in this predator-prey relationship. Measurements of prey populations are again lacking; there is reason to believe, however, that the densities of pocket gophers on Nebraska National Forest and on the uplands of the Valentine Lakes area were about the same, at least not six times as great on the former as on the latter, which might seem to be indicated by the 6:1 ratio of gopher remains in coyote seats from these two areas, respectively. The high occurrence value of remains of *Microtus* in seats from the Valentine Lakes area, where it was by a wide margin the most frequently represented food item, may be significant here. Large numbers of meadow mice in the marshy areas and their diurnal activities along obvious runways making for easy capture, apparently attract foraging coyotes away from the higher and drier habitat of the pocket gopher in this situation.

The pocket gopher ranked first in the diet of the coyotes on Nebraska National Forest (Fig. 17). This may be of more than academic interest. The Forest Service apparently considered the pocket gopher population on the Bessey Division to be at a dangerous density, inasmuch as a "control" team was operating there during the period of this study. *Geomys* girdles or cuts off young conifers just below the soil surface, and efforts to control this rodent were applied on 464 ac in 1947, and 1,956 ac in 1948. The following figures present some interesting possibilities.

In 1947 and 1948, Forest Service personnel estimated the number of coyotes resident on the Bessey Division at 400. By 1949, coyotes appeared to be increasing and the estimated population was 450. Data furnished by Murie (1946) would indicate that a coyote feeding on small wild mammalian prey would drop a daily average of about six seats. In this connection, coyotes on our study areas were seen defecating during early morning and early afternoon, and after sundown. Under usual field conditions, then, a coyote would drop about 2,190 seats in a year. On the basis of experimentation, Murie (1946) believes that, in analyzing coyote droppings, "there probably is slight chance of duplication in the total tally of prey, up to the size of a squirrel," indicating that, where large numbers of seats are studied, a unit seat containing remains of pocket gopher can be considered as representing one gopher eaten. Pocket gopher remains appeared in 45% of the 1,740 seats gathered on the Bessey Division (Table 9 and Fig. 17). Using these figures, it may be estimated that the 400 coyotes on this area during the study annually dropped 876,000 seats, 45% of which contained remains of pocket gopher, indicating an annual consumption of 394,200 gophers by coyotes, an average of 4.3 gophers per ac. Because an unusual local abundance of a prey species may attract predators, it is possible that the annual take per acre by coyotes was well above this figure in the potential "gopher trouble" spots among the Forest plantations. Murie



TABLE 9. Seasonal and areal percentages of occurrence of food groups and items in 2159 coyote seats collected in sandhills study areas in Nebraska from February 26, 1947 to March 20, 1951. For footnotes, see below Table 8.

Food groups and items	SANDHILLS STUDY AREAS									
	NEBRASKA NATIONAL FOREST					VALENTINE LAKES AREA				
	912	572	176	80	1740	277	126	0	16	419
Number of seats.....	Win-ter	Spring	Sum-mer	Au-tumn	All	Win-ter	Spring	Sum-mer	Au-tumn	All
MAMMAL.....	97.7	96.2	90.3	76.3	95.5	98.9	99.2	...	100.0	99.0
SMALL WILD MAMMAL.....	86.3	81.6	62.5	58.8	81.1	95.7	96.8	...	100.0	96.2
Rabbit-mouse-pocket gopher.....	85.5	80.4	60.2	56.3	79.9	93.1	79.4	...	93.8	89.0
Rabbit.....	16.3	15.2	9.1	3.8	14.7	35.0	11.1	...	25.0	27.4
<i>Sylvilagus</i> .....	1.8	2.1	0.6	0.0	1.7	15.5	4.0	...	0.0	11.5
<i>Lepus</i> .....	5.7	3.8	2.3	0.0	4.5	4.7	0.0	...	12.5	3.6
Undetermined rabbit.....	8.9	9.3	6.3	3.8	8.5	14.8	7.1	...	12.5	12.4
Mouse.....	60.0	58.4	39.2	36.3	56.3	75.8	74.6	...	87.5	75.9
<i>Microtus</i> .....	32.8	38.1	17.6	16.3	32.2	69.7	58.7	...	81.3	66.8
<i>Reithrodontomys</i> .....	16.1	6.6	3.4	8.8	11.4	2.9	1.6	...	6.3	2.6
<i>Peromyscus</i> .....	1.1	1.7	0.6	1.3	1.3	0.4	0.0	...	0.0	0.2
<i>Dipodomys</i> .....	6.7	4.9	2.3	6.3	5.6	3.2	4.0	...	0.0	3.3
<i>Perognathus</i> .....	3.1	5.4	8.0	11.3	4.8	1.1	4.0	...	6.3	2.1
Other genera.....	0.0	0.0	0.0	0.0	0.0	0.0	0.0	...	0.0	0.0
Undetermined mouse.....	17.1	13.6	15.3	13.8	15.6	9.4	15.1	...	6.3	11.0
Pocket gopher ( <i>Geomys</i> ).....	46.6	48.6	33.0	36.3	45.4	6.9	8.7	...	12.5	7.6
<i>Onychomys</i> .....	1.3	2.4	0.6	1.3	1.6	18.4	45.2	...	31.3	27.0
Other genera <sup>1</sup> .....	2.6	3.1	8.5	1.3	3.3	5.1	1.6	...	6.3	4.1
DEER.....	15.6	7.2	2.3	0.0	10.7	0.0	0.0	...	0.0	0.0
DOMESTIC MAMMAL.....	32.2	37.1	51.7	18.8	35.2	18.4	13.5	...	0.0	16.2
Cow.....	31.8	37.1	51.7	18.8	34.9	18.4	13.5	...	0.0	16.2
Sheep.....	0.0	0.0	0.0	0.0	0.0	0.0	0.0	...	0.0	0.0
Horse.....	0.3	0.0	0.0	0.0	0.2	0.0	0.0	...	0.0	0.0
Pig.....	0.1	0.0	0.0	0.0	0.1	0.0	0.0	...	0.0	0.0
Undetermined mammal.....	4.1	5.4	20.5	17.5	6.8	4.7	2.4	...	6.3	4.1
BIRD.....	26.6	27.4	48.9	13.8	28.6	39.0	23.0	...	31.3	33.9
Wild Bird.....	26.6	27.4	48.9	13.8	28.6	39.0	23.0	...	31.3	33.9
Galliformes.....	14.3	13.8	9.7	7.5	13.3	17.3	1.6	...	0.0	11.9
Pheasant.....	3.3	3.0	2.3	0.0	2.9	9.0	0.8	...	0.0	6.2
Grouse <sup>2</sup> .....	7.0	5.1	4.0	2.5	5.9	5.1	0.8	...	0.0	3.6
Undetermined.....	4.1	6.1	3.4	5.0	4.7	3.6	0.0	...	0.0	2.4
Duck.....	0.3	0.2	0.0	0.0	0.2	6.9	3.8	...	0.0	5.5
Small bird <sup>3</sup> .....	2.2	4.7	22.7	3.8	5.2	1.4	1.6	...	6.3	1.7
Undetermined.....	10.5	9.1	17.0	2.5	10.3	14.1	16.7	...	25.0	15.3
DOMESTIC CHICKEN.....	0.0	0.0	0.0	0.0	0.0	0.0	0.0	...	0.0	0.0
REPTILE <sup>4</sup> .....	4.3	9.3	15.9	2.5	7.0	0.0	4.0	...	0.0	1.2
AMPHIBIAN <sup>5</sup> .....	0.0	0.2	0.0	0.0	0.1	0.0	0.0	...	0.0	0.0
FISH.....	0.0	0.0	0.0	0.0	0.0	0.0	2.4	...	0.0	0.7
Undetermined vertebrate material.....	1.0	1.2	1.1	1.3	1.1	0.4	0.8	...	0.0	0.5
Egg shell <sup>6</sup> .....	0.9	4.4	8.0	0.0	2.7	1.1	0.8	...	0.0	1.0
INSECT <sup>7</sup> .....	23.0	30.4	80.7	50.0	32.5	1.4	12.7	...	12.5	5.3
PLANT MATERIAL.....	39.4	36.7	56.8	85.0	42.4	17.3	15.9	...	56.3	18.4
Fruit <sup>8</sup> .....	22.8	5.2	15.3	80.0	18.9	0.7	4.0	...	50.0	3.6
Grass.....	18.2	29.0	47.2	17.5	24.7	16.2	11.1	...	18.8	14.8
Other <sup>9</sup> .....	4.7	4.0	2.8	3.8	4.3	1.1	0.8	...	0.0	1.0
Undetermined material.....	0.2	0.3	0.0	0.0	0.2	0.0	0.0	...	0.0	0.0
Non-food material.....	1.3	3.0	0.6	0.0	1.7	0.4	0.8	...	0.0	0.5

(1935) found indications that the coyote in Jackson Hole "deliberately seeks" the pocket gopher "as a staple food." Murie (1940) was of the opinion that in Yellowstone Park the coyote was "the greatest single factor in keeping the pocket gopher population within safe bounds."

*Geomys* was well represented in seats during all seasons (Figs. 24 and 25), the lumped data showing a spring high slightly more than 3% above the annual average and a summer low somewhat more defined. Seasonal percentages of pocket gopher occurrences in seats over a period of about 30 months depicted in chronological order (Fig. 25) twice show the slight trend upward in spring, but in 1949 the winter-to-spring trend was slightly downward. There seems to be some correlation in all cases with the opposite winter-to-spring trend in utilization of galliform birds. The summer lows are probably correlated with increased use of insects (Fig. 25) and cow (Figs. 21 and 25). That coyotes feed quite heavily on the subterranean pocket gopher in winter in this area might at first seem unlikely. *Geomys* remains active throughout much of the winter, however, numerous earth cores evidencing its operations under snow which apparently often falls before extensive freezing of the sandy soil has occurred. The very heavy snows in the winter of 1948-49 caused only a moderate trough in the utilization of pocket gopher, whether directly or indirectly.

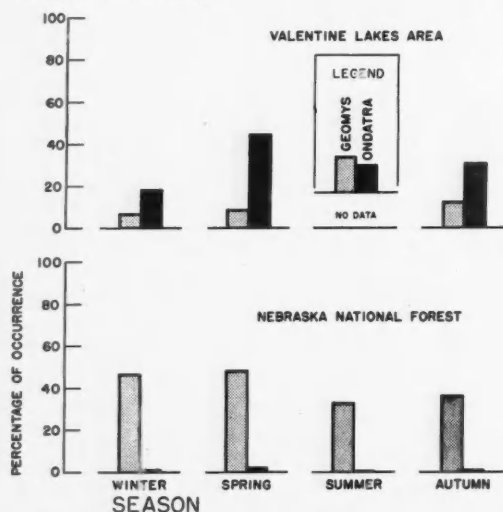


FIG. 24. Seasonal percentages of occurrence of remains of *Geomys* and *Ondatra* in 1,740 coyote seats from a xeric sandhills habitat (Nebraska National Forest) and in 419 seats from an area of lakes and marshes in the sandhills (Valentine Lakes Area).

#### Muskrat

The muskrat (*Ondatra zibethica*), found in aquatic habitats throughout Nebraska, was represented in stomachs and seats from the sandhills only (Table 5 and Fig. 16). It assumed the proportions of an important food item in the coyote's diet only on the

Valentine Lakes area where its remains were found in 27.0% of 419 seats (Fig. 17). Because it ranked equally with rabbit which is a lumped item of two genera, muskrat can be considered as ranking second only to the meadow mouse on the coyote's menu in this sandhill-marsh situation.

In an effort to learn something of the importance of the muskrat in the diet of coyotes, as a part of his intensive studies on muskrats within the Valentine National Wildlife Refuge, Sather picked up a total of 212 coyote seats along the shore of Pony Lake during the spring of 1950, the winter of 1950-51, and the spring of 1951. All seats were collected within 100 yd of the lake margin. Pony Lake was supporting a top-heavy population of muskrats, most of which lived in bank dens; trappers made little or no attempt to harvest them. It is impossible, of course, to know definitely whether muskrat remains found in seats collected on a given restricted area represent muskrats taken in that area, but observations of hunting behavior seemed to indicate that individual coyotes regularly hunted certain marshes. Outstanding in this series of seats, as well as in all those taken on the Valentine Lakes area (Table 9 and Fig. 24), is the spring peak in percentage of occurrence of muskrat remains. This high in the seasonal pattern of the coyotes' utilization of muskrats coincides with the muskrat's spring period of dispersal from wintering to breeding quarters, territorial disputes, and the cross-country movements which take these furbearers away from their natural aquatic habitat, sometimes miles from the nearest water. It appears, therefore, that sandhills muskrats are, under usual climatic conditions, most vulnerable during early spring.

The inverse patterns of occurrence of meadow mouse and muskrat representations in seats, previously noted in the section on *Microtus*, was evident in the Pony Lake series (Figs. 22 and 24). As the frequency of meadow mouse remains went up in the winter, the occurrence of muskrat declined. The reverse pattern occurred in the spring. Very high values for the frequency of meadow mice, plus the second place rating of muskrat among generically grouped food items, as compared to the occurrence of remains of the typically upland pocket gopher, strongly indicates that coyotes on the Valentine Lakes area were concentrating their hunting along the lake margins and in the marshes and wet meadows.

The heavy snows of the winter of 1948-49 presented a good opportunity to observe the hunting behavior of coyotes on a marsh. On the afternoon of January 12, three coyotes were observed by Sather on the ice at Ballard's Marsh. It was possible to follow their actions closely from a distance with the aid of binoculars. There was no indication they had noticed the observer's presence in the vicinity. They made what appeared to be a routine visit to most of the muskrat houses. They did not attempt to dig into any of the houses, but they did urinate on many of them. After visiting the muskrat houses, they spent most of approximately an hour in heavy stands of river bulrush

and sedge where meadow mice were known to be abundant. Occasional pounces followed by probing actions with the nose indicated they were mousing.

Three coyotes, presumably the same trio, were observed hunting on January 13, 14, 21, and 26. They continued to visit the muskrat houses, but did not disturb any. Definite evidence that a coyote had caught and killed a muskrat was found on January 27. The sign indicated that the muskrat had been sitting in a fragile push-up feeder when attacked. Three days later a feeding house was found that had been opened by coyotes; another was found on February 1. There was no evidence that the coyotes had successfully preyed upon muskrats by opening these houses.

A close correlation was found between the occurrences of muskrat disease and damage to houses by coyotes during the winter months. On February 15, 1950, a trapper found a muskrat dead in a house on West Long Lake; the animal exhibited the typical symptoms of the hemorrhagic muskrat disease. An examination of the lake on the same date revealed that most of the houses had been opened by coyotes. A few houses were still intact, and four victims of the disease were found in these houses. Mr. Harold Miner, a state trapper, took a few muskrats on Ballard's Marsh in January 1952, returning in February to complete the harvest. During the January trapping, no dead muskrats were found in houses, and no houses had been molested by coyotes. When trapping was resumed in February he found a number of dead muskrats in houses and many houses that had been opened by coyotes.

Dr. Paul Errington (correspondence, 1949) relates that trappers in the vicinity of the Malheur National Wildlife Refuge in Oregon regard the digging into lodges by coyotes as indicative of dead muskrats within. Observations on the Valentine Lakes area point to the conclusion that, during the winter, coyotes do not ordinarily prey upon muskrats by opening houses. Certain individuals that are once successful in capturing an animal in such a manner may continue to use the same method. Most houses molested by coyotes probably contain dead muskrats.

#### Deer

In 1914, it was estimated that eight mule deer (*Odocoileus hemionus*) were resident on the Bessey Division of Nebraska National Forest. The population of deer increased to an estimated 630 by 1940, and it had become apparent that herd reduction measures would soon be needed to keep the animals' numbers within the biological limits of the range, and to protect the forest plantations. The history of knowledge about mule deer in Nebraska, the nature of the range on the Bessey Division, the composition of the herd there, and other findings furnished by a controlled hunt conducted in December, 1945, have been reported (Mohler, Wampole & Fichter 1951). In this unique situation, an expanding, man-planted forest of conifers within a vast and near-primitive

sandhill grassland, the relationships of coyotes with such a deer population are of special interest.

Mule deer returned to much of Nebraska during the two or three decades just past. Occurrence of deer remains in coyote stomachs was, however, virtually negligible generally, being highest (3.1%) in stomachs from the western high plains, although comprising but 0.1% of the total volume of contents. Its remains in seats were found only in those collected on Nebraska National Forest and with a frequency of 10.7% (Fig. 17). Lumping the seasonal data for occurrence of deer remains in seats indicates a general seasonal trend (Fig. 21). While this pattern of winter high sloping to an autumnal low may be more or less reliable in broad outline, it does not tell the whole story. Arrangement of available and pertinent climatic data chronologically (Fig. 25) shows that coyotes on the Bessey Division very infrequently ate deer, except during the latter part of the winter of 1948-49 when a spectacular peak of deer remains in seats resulted from emergency conditions—a peak responsible for the apparent magnitude of the generalized winter high shown in Figure 21 as derived from lumped seasonal data. The blizzards of January, February, and March of 1949 were the worst ever recorded for Nebraska. High winds, heavy snowfall, and unusually low temperatures in combination caused widespread hardship. Livestock losses were staggering; many thousands of cattle died on the range.

A record snowfall of 86 in on the Bessey Division was clearly accompanied by a dramatic increase in the intake of deer by coyotes. What the graph shows was apparent qualitatively to the seat collector on the Forest; seats obviously composed entirely or largely of deer hair became common late in the winter of 1948-49. What proportions of those occurrences represented remains of deer killed by coyotes and of deer killed by other causes cannot be ascertained. In view of the severity of the blizzards and the enormous losses of cattle in the sandhills due to the weather, it is probable that most of the deer remains in coyote seats that winter and early spring came from carcasses of "winter-killed" deer or weakened individuals that the coyotes could easily kill. Our data are handicapped by a paucity of field observations in the light of which to interpret the laboratory findings. Any interpretation would, of course, be evaluated intelligently only in relation to the population density of the deer, the condition of their range, and its potential carrying capacity.

Coyotes do attack apparently healthy deer in this area. Forest Ranger M. F. Brandborg (correspondence, 1947) reported that early in the afternoon of March 15, 1947, he was notified that two coyotes were attacking an adult deer about 5 mi west of Halsey and between the highway (Nebraska 2) and the nearby Middle Loup River. Accompanied by Mr. John Maslak, he immediately drove to the site. They saw no coyotes, but sighted a wet and "rather bedraggled-looking" deer bedded down in the brush

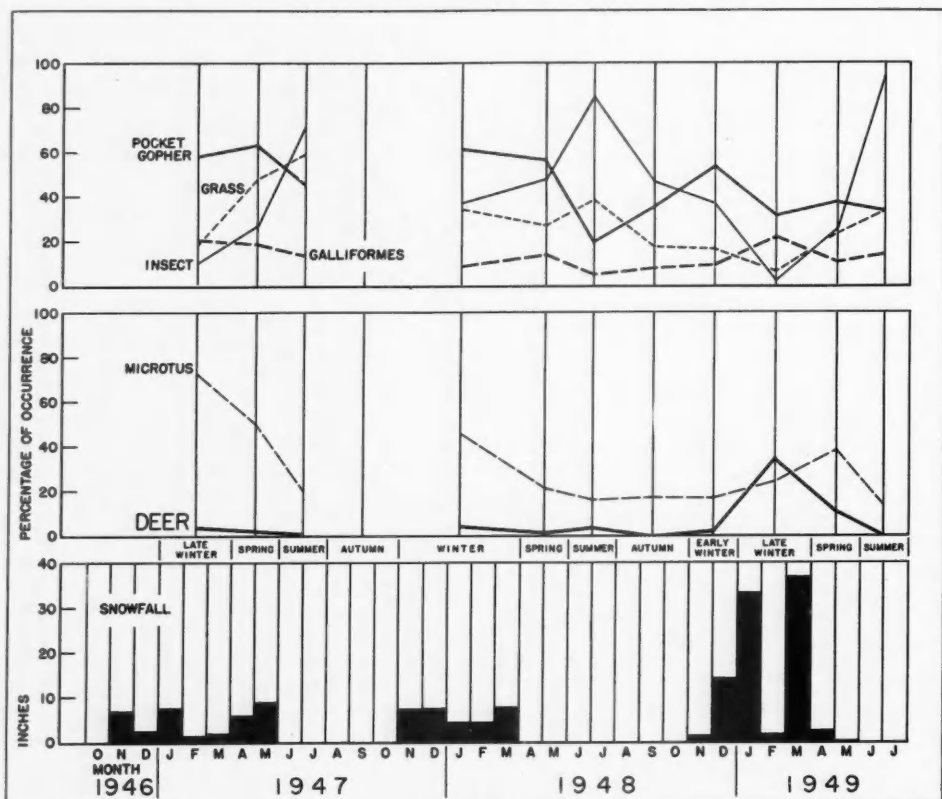


FIG. 25. Correlation of (1) seasonal percentages of occurrence of remains of deer and certain other food groups and items in coyote scats found on Nebraska National Forest, February 1947 through the summer of 1949, and (2) monthly snowfall as recorded at nearby Halsey, Nebraska (see Fig. 26). Total snowfall for the three winters: 1946-47, 20.8 in; 1947-48, 33.1 in; 1948-49, 88.1 in.

just south of the river. They returned to the spot later in the day and found a large doe feeding, apparently in good condition. She had a long but apparently shallow cut, which had stopped bleeding, high on and toward the median surface of the right hind leg. Although the leg seemed a little stiff, the doe was walking on it apparently without trouble. It can be conjectured that the two coyotes had been unable to get her down and had abandoned the attack when she succeeded in crossing the river.

Coincident with the greatly increased utilization of deer by coyotes in the winter of 1948-49 was the appearance of a horizontal gradient in the frequency of deer hair in scats within the tract. Percentages of occurrence of deer remains determined for scats taken along each of three segments of the 15 mi of graveled road revealed the values shown in Figure 26. That segment of the road depicted as a heavy, solid line (A) is about 9 mi long; much of it transects the more heavily timbered portions where the plantations, at that time, ranged from about 10 to 45 yrs old (Fig. 3). The stretch of road shown checkered (B) comprised the three-mile "scat run," through somewhat

more scattered and younger stands, open timber, new plantations, and into the unplanted area. About  $3\frac{1}{2}$

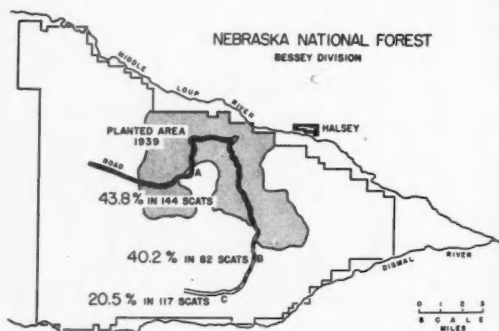


FIG. 26. Generalized map of the Bessey Division of Nebraska National Forest, showing (1) the approximate area planted to conifers as of 1939, (2) the graveled work road along which coyote scats were collected, and (3) the percentages of occurrence of remains of deer in coyote scats taken on three segments of the road late in the winter of 1948-49.



mi of road, shown as a double line (C) is in open grassland, well away from the plantations (Fig. 2).

These data suggest that the consumption of deer, whether killed by coyotes or secured as carrion, or both, was twice as high among the coniferous plantations as in the open grassland. Deer in Nebraska National Forest tend to move into the more heavily timbered areas, even in mild winters (Mohler, Wampole & Fichter 1951). It is problematical whether these data indicate that some coyotes were hunting wholly or largely inside the planted area and others wholly or largely outside. If such "microgeographic" differences in feeding patterns can occur, the need for detailed studies on this predator, and for the minimal area requirements of such studies, is emphasized.

#### *Domestic Mammals*

Remains of domestic mammals, i.e., cow, horse, sheep, and pig, were found in 26.1% of all stomachs examined and made up 12.5% of the total volume of food materials. These remains were largely those of cattle and hogs. No attempt was made to distinguish carrion, or to segregate representations of young and mature animals. Many of the remains almost certainly represent carrion which can come from the carcasses of either young or mature animals. Many farmers do not bury or burn dead young pigs, for example, but make them available to scavenging coyotes by carrying them into fields or by simply tossing them a short distance from the breeding pens. During the winter of 1948-49, coyotes repeatedly visited the carcasses of two or three pigs (probably about one-fourth grown) that had been dropped into a small gully on the Valley County study area. Coyote tracks leading to the spot and the disturbance in the snow occasioned by the coyotes' efforts to chew on the frozen carrion, attracted attention to the spot. A dead horse with a part of one flank eaten away was found in a pasture on this study area on April 7, 1948; by November 7, many of the bones were scattered but coyotes were still chewing at the dried skin and tags of connective tissue. Two coyote seats were collected at the site on the latter date. On May 11, 1949, a "well-cleaned" carcass of a yearling whiteface was found in a sweet clover patch on the Valley County study area.

Although not evident in our findings, depredations of coyotes upon sheep do create serious, local, economic problems in the high plains. For example, 300 ewes and lambs were reported killed by coyotes between the falls of 1942 and 1943 on a 1600 ac ranch in Dawes County, Nebraska.

#### *Cow*

Representations of cow generally yielded higher values in both stomachs and seats than those of any or all other domestic mammals except in the loess land types where it was slightly exceeded by pig in stomach contents and considerably outranked by pig in winter seats. Stomach analyses showed that cow was more important to coyotes in the high plains and sandhills

than in any other land type, and most prominent in the carnivore's feeding patterns in the sandhills (Fig. 18). In 1941 the population of cattle was depicted as being slightly less dense in the sandhills than in the loess hills (Anonymous 1941). Evidence of cow was found in 28.4% of all seats examined (Fig. 15), but appeared in nearly four times as many coyote droppings from the sandhills as in those from loess hills (Fig. 16). Cow was apparently twice as important in Nebraska National Forest, where remains were found in 34.9% of the seats, as it was in the Valentine Lakes area.

Most of these occurrences probably represent carrion. It is believed that coyotes rarely if ever kill mature cattle, or even try. Sather watched two coyotes near a herd of cattle north of the Valentine Lakes area on February 3, 1949. One coyote walked through the herd, none of which paid any attention to it. The other coyote stopped to investigate something on the ground near the cattle. A cow walked toward him; he quickly moved out of the way and soon afterward disappeared. Calves are sometimes vulnerable to attack and coyotes occasionally kill them. One sandhill rancher indicated in conversation that he annually lost about one per cent of his calves to coyote predation.

The seasonal pattern of cow remains in all coyote seats analyzed (Fig. 19) is influenced by the pattern shown by the sandhill seats (Fig. 20) which, in turn, is apparently a function of the seasonal pattern in Nebraska National Forest (Fig. 21), the summer value in the Valentine Lakes area not having been ascertained. It is notable, however, that the annual peak of consumption of cow by coyotes occurred in the summer in both sandhills and loess hills, although less pronounced in the latter. Cow is the only one of the principal mammalian food items that shows a spring-to-summer increase; all others decline.

The relationship of the seasonal pattern of cow remains in seats to the seasonal sequence of numbers of cattle present on the Bessey Division is shown in Figure 27. These graphically portrayed values represent the number of cattle on 20 allotments within which all seat collecting for this area was done. Most of the cattle were moved onto the Forest from May 16 to June 1 in each of the three years during which studies were in progress. Removal of cattle began on October 15 in both 1947 and 1948, and continued, as shown, into the winter. After February there are usually no cattle on the forest, excepting a few strays. Extensions of grazing rights in 1947 carried 245 head of cattle on two allotments until January 1, 1948, and 45 head on one allotment for two more months.

Four features are outstanding in Figure 27: (1) The steady winter-to-summer increase in percentage of remains of cow in coyote seats in 1947 and 1948 (see also Table 10), although the advent of virtually the entire population of cattle took place each spring in 15 days. This may represent a gradual increment of dependence upon cow as carcasses become available through agencies other than the coyotes themselves.

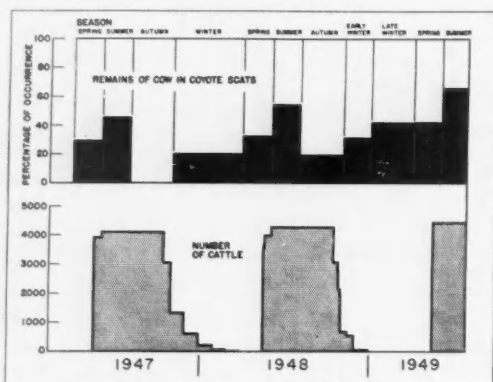


FIG. 27. Seasonal percentages of occurrence of remains of cow in 1,602 coyote seats in Nebraska National Forest during a period of 852 days, and the chronological distribution of numbers of cattle in the grazing allotment areas in which seat collections were made during the same period. Data for autumn 1947 lacking.

(2) The sharp decline from summer to autumn in 1948 (autumnal figures for 1947 unfortunately lacking) although cattle were still present in large numbers through the autumn. The well-defined increase in the incidence of pocket gopher remains in seats at that time (Fig. 25) may be correlative. It may be that mortality among the cattle was greatest during

the spring and early summer and that the quantity of carrion was decreasing quite rapidly by the end of summer. (3) The increasing height of the summer peak through the three years accompanying only slight increases in the number of cattle. (4) The pattern for the winter of 1948-49 and the following spring apparently reflect certain drastic biological effects of severe winter weather. An increased utilization of cow is definitely clear, comparable to that of deer (Fig. 25), whether by virtue of greater availability as a function of more carcasses, or because of decreased availability of pocket gophers (Fig. 25) in the presence of the usual number of cow carcasses and the pressure of necessity.

In 1948, when the maximum number of cattle on the allotments considered here was 4,316, the ranchers involved reported a total of three head strayed or lost, ten killed by lightning, and one calf killed by coyotes. Other coyote kills may, of course, have gone undetected. Some calving takes place on the Forest. There is little or no doubt, however, that the relatively high and seasonally fluctuating frequency of cow remains in seats (surpassing all other items except insect in summer), reflecting the importance of cattle in the feeding pattern of the coyotes in this area, is made possible by the presence of carrion.

The carcass of a cow can obviously furnish material for a large number of coyote droppings. It would appear that a carcass can, for a considerable period, continue to furnish material which, when found

TABLE 10. Seasonal percentages of occurrence of certain food groups and items in 1650 coyote seats in chronological sequence as collected on the Bessey Division of Nebraska National Forest, from February 26, 1947 to July 7, 1949.

Food groups and items	Number of seats	1947				1948					1949		
		Late winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Early winter	Late winter	Spring	Summer
		48	152	72	*	268	119	75	75	176	343	301	21
MAMMAL		100.0	95.4	94.4	...	97.0	95.8	85.3	78.7	95.5	98.8	96.7	95.2
SMALL WILD MAMMAL		95.8	87.5	68.1	...	93.3	79.8	65.3	60.0	88.1	79.9	78.1	71.4
Rabbit-mouse-pocket gopher		93.8	86.2	65.3	...	92.9	78.2	65.3	57.3	87.5	79.9	76.7	61.9
Rabbit		20.8	19.1	12.5	...	19.0	17.6	8.0	4.0	9.7	17.8	12.3	0.0
Mouse		79.2	57.9	34.7	...	56.3	49.6	38.7	38.7	63.1	53.4	63.1	47.6
Microtus		72.9	50.7	20.8	...	45.5	21.8	16.0	17.3	17.0	23.9	38.2	14.3
Pocket gopher ( <i>Geomys</i> )		58.3	63.8	45.8	...	61.6	56.3	20.0	36.0	54.0	31.5	37.9	33.3
DEER		4.2	2.6	1.4	...	4.5	1.7	4.0	0.0	2.8	35.0	11.6	0.0
Cow		18.8	29.6	45.8	...	20.9	32.8	54.7	20.0	33.5	42.3	42.5	66.7
BIRD		41.7	34.9	44.4	...	14.6	31.9	53.3	14.7	21.0	36.4	22.3	57.1
Galliformes		20.8	19.1	13.9	...	9.0	14.3	5.3	8.0	9.7	22.2	11.0	14.3
Pheasant		2.1	4.6	1.9	...	2.2	3.4	0.0	0.0	2.3	5.2	2.0	14.3
Grouse		4.2	5.9	8.3	...	2.6	4.2	1.3	2.7	5.7	12.5	5.0	0.0
Undetermined		14.6	8.6	4.2	...	4.1	6.7	4.0	5.3	1.7	4.7	4.7	0.0
INSECT		10.4	27.0	72.2	...	37.3	47.9	85.3	46.7	36.9	2.6	25.2	95.2
FRUIT		4.2	0.0	18.1	...	23.5	6.7	17.3	82.7	53.4	8.4	6.6	4.8
Grass		18.8	48.0	59.7	...	34.3	26.9	38.7	17.3	16.5	6.7	23.6	33.3

in laboratory analysis of seats, yields no clue other than that it is "cow." On October, 1946, a mature whiteface cow died near the south end of the "seat run" in the Bessey Division. Within four days, according to Forest Ranger M. F. Brandborg, the carcass was nearly cleaned of flesh by coyotes. Fichter visited the site on April 30, 1947, and found the skeleton relatively intact, tags of connective tissue clinging to the bones, a rather large amount of hide with the hair persisting, and several coyote seats. Evidence observed on July 15 and 16 indicated that coyotes were still chewing at this carcass of a cow that had died nine months before. On March 1, 1948, fresh tracks in about 2 in of snow that had fallen the night before showed that a coyote had visited the bones and chewed briefly on the skeletal remains, now 18 months old. For at least nine months, and probably longer, coyotes could get cow hair into their digestive tracts from this carcass. This evidence undoubtedly accounts for the continuing appearance of cow remains in many seats during periods when cattle were virtually absent from the area. Furthermore, and perhaps of greater significance, here is evidence that laboratory findings are largely purposeless, even misleading, without the tempering influence of correlated observations in the field.

#### BIRDS

In evaluating the significance of bird remains in the stomachs and seats of predators, attention is usually directed to three categories, poultry, game birds, and non-game birds (Sperry 1941). In this report, the avian food group, which ranks second in quantitative importance in the coyote's basic feeding pattern, is first divided into wild bird and domestic chicken (i.e., poultry, which here includes one known occurrence of domestic turkey); wild bird is thence divided into Galliformes, ducks, and small bird, the first two constituting game species, the last being equivalent to the non-game bird category of other authors. Pheasant and grouse furnished the only galliform remains recognizable beyond the ordinal rank.

The relatively high percentages of undetermined bird remains are regrettable, but were unavoidable because of technical limitations. The system of categorization used here may slightly compensate for this weakness. Furthermore, it seems reasonably certain that most avian remains classified as "undetermined wild bird" were those of non-game species or "small bird."

On a statewide basis, wild bird remains occurred in about twice as many stomachs as did domestic chicken, but these two sources of food comprised essentially the same percentages of volume, i.e., 8.8% and 8.9%, respectively. Stomach contents indicated that wild birds were most important to coyotes in the western high plains and the loess land types, and that gallinaceous forms furnished most of the wild bird material with a remarkable uniformity of values through these three land types (Tables 5 and 6).

Representations of duck in both stomachs and seats

presented only minor values except in seats collected on the Valentine Lakes area where a frequency of 6.9% in 277 winter seats furnished the highest of the three seasonal values determined for that area (Table 9).

The seasonal pattern of utilization of wild birds, as determined by frequency of remains in seats from the sandhills and loess hills (Figs. 31 and 32), focuses some interest upon the small bird category. The marked summer peak is in part forced by a summer high in the incidence of small bird remains in seats from both loess hills and sandhills, more pronounced in the latter. This peak may indicate an increased availability of small birds by virtue of ground nesting species, and the areal difference may reflect a denser population of birds nesting on the ground and in low shrubs in the grasslands of the sandhills than in the farmlands of the loess hills. The only determinable remains of small birds found in seats from the sandhills were of meadowlark and mourning dove, both ground nesting species.

Murie (1941) indicated that "birds are usually taken accidentally" by coyotes in Yellowstone Park, presumably meaning that birds are fed upon only when found "accidentally" and easily caught. It is probable that the coyote rarely hunts small bird prey with the persistence and in the systematic manner it employs in catching pocket gophers and meadow mice.

Ducks and small birds appear to be so relatively unimportant in the feeding patterns of coyotes in Nebraska that attention is focused on the Galliformes, the pheasant and grouse because of their value as game species, domestic chicken for economic reasons.

#### Pheasant

Pheasant was represented in 14.9% of the 747 stomachs and made up 7.4% of the total volume of food present. Its percentage of occurrence was highest (20.9%) in stomachs from loess plains, but only slightly less in those from loess hills (19.8%) and high plains (18.8%). These closely conforming values (Fig. 18) are of interest in relation to a map published in 1946 (Anonymous 1946) showing the "better spots in Nebraska for hunting pheasant." On that map, four heavily shaded spots indicate the areas of heaviest pheasant population; two were in loess hills, one in loess plains, and one in the western high plains. The percentage of volume yielded by pheasant in stomachs from the high plains was considerably less than in those from the loess types (Fig. 18). Values for pheasant in sandhill stomachs was somewhat intermediate, and virtually nil in the drift hills where pheasant numbers are low.

Of 2,500 coyote seats, only 6.4% contained pheasant remains (Fig. 28). This overall value loses significance, however, when an areal breakdown of the data is made (Fig. 29); the pattern of difference in frequency values in seats from the two land types is most striking, and the role of the pheasant in the diet of coyotes in the loess land types is again spotlighted.

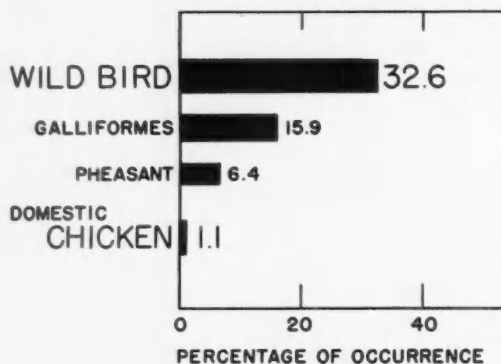


FIG. 28. Percentages of occurrence of certain avian food groups and items in 2,500 coyote seats collected in Nebraska.

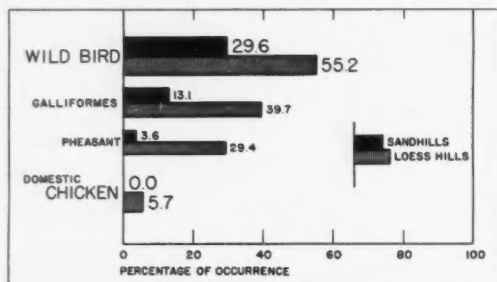


FIG. 29. Percentages of occurrence of certain avian food groups and items in 2,159 coyote seats collected in sandhills and in 194 seats taken in loess hills.

Large numbers of pheasants winter in the marshy valleys of the Valentine Lakes area, whereas they are at all times relatively scarce on Nebraska National Forest. The rates of utilization by coyotes on the two areas (Fig. 30), and especially the winter high of 9.0% on the Valentine area (Fig. 33), apparently reflect these conditions.

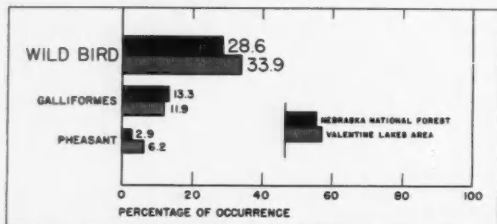


FIG. 30. Percentages of occurrence of certain avian food groups and items in 1,740 coyote seats from a xeric sandhills habitat (Nebraska National Forest) and in 419 seats from an area of lakes and marshes in the sandhills (Valentine Lakes Area).

Counts of pheasant cock calls, in 2 min listening periods as standardized for securing index values relative to breeding populations, were frequently made by Fichter in the course of field work. The highest counts made on the study areas offer interest-

ing comparisons with the over-all percentages of occurrence of pheasant remains in coyote seats from the same biotic complexes. On Nebraska National Forest, 10 pheasant cock calls and 2.9% frequency of pheasant remains in seats; on the Valentine Lakes area, 63 calls and 6.2%; for the loess hills, 104 calls and 29.4%.

The pheasant provides an important food item in the menu of the coyote in the loess hills and plains. In the loess hills its frequency of occurrence in all seats examined was equal to that of meadow mouse and nearly half that of rabbit. Notes on some possibly pertinent observations made in this land type would seem, therefore, to be in order.

Conspicuous in the seasonal pattern of the coyote's utilization of pheasants in the midst of heavy populations of the bird was the lack of wide seasonal fluctuations (Fig. 32) except for the shift from the autumnal low of 21.7% to the winter high of 36.6%. Certain expectations were not borne out by the data gathered. "It stands to reason" that coyotes eat more pheasants during the spring when nesting hens are more vulnerable to predation, was an opinion often heard expressed among sportsmen and farmers in the loess hills country. Biologists cautioned that, if pheasant remains in seats of coyotes did produce a spring or early summer peak, it must be remembered that the first mowing of alfalfa, in which pheasants commonly nest, kills and maims many hens, and that remains of those birds in seats could rarely if ever be distinguished from remains of pheasants killed by coyotes. On and in the vicinity of the Valley County study area, from one to several hens were injured or killed by power mowers in every patch of alfalfa visited by Fichter during the late May cutting in 1948. Here was seeming evidence of increased availability of pheasant meat. Neither it, nor the supposedly increased vulnerability of hens on nests

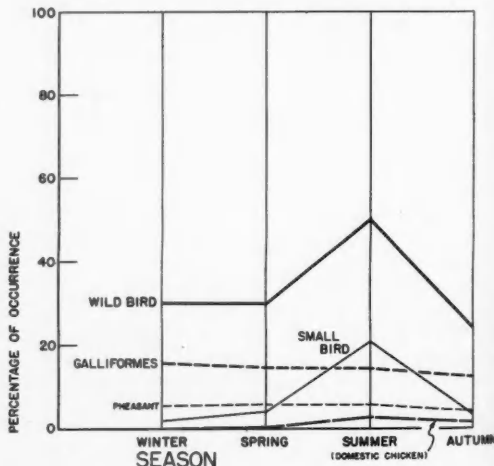


FIG. 31. Seasonal trends of certain avian food groups and items represented in 2,500 coyote seats collected in Nebraska.



was reflected in the data derived from coyote seats. There was instead a slight winter-to-spring decline. These findings might suggest (1) that pheasant hens are not more vulnerable when nesting and may, indeed, be less vulnerable, (2) that coyotes do not intentionally seek out nesting pheasants, and (3) that most of the pheasant flesh eaten at any season is carrion.

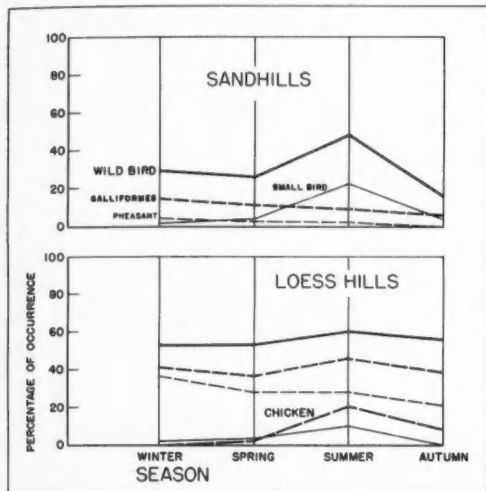


FIG. 32. Seasonal trends of certain avian food groups and items represented in 2,159 coyote seats collected in sandhills and in 194 seats taken in loess hills.

Because of reports that pheasant remains were commonly conspicuous about breeding dens of coyotes, den refuse studies were included among the early efforts on the coyote-pheasant problem. They looked promising at first, but were abandoned when observations on coyote behavior (Fichter 1950) indicated that values furnished by den refuse might be misleading. Watching coyote pups about breeding dens disclosed that much of the time they chew on anything available. This led to a closer examination of den refuse and the reasonably reliable conclusion that lingering remains of mammalian prey, particularly cottontail, are frequently eliminated by continued feeding, whereas the wings of gallinaceous birds tend to persist and thereby accumulate a source of over-weighted evidence.

Coyote pressure on pheasant populations during the nesting season may be significantly heavier upon the contents of the nests than upon the incubating birds. Out of 11 pheasant nests located by search or by chance on the two study areas in loess hills and kept under observation during the period of April 26 to June 26, 1947, five had been destroyed by mammals when found, and one was destroyed by a mammal after it had been discovered. Sign, including tracks, hair, and the presence or absence of digging in the nest cavity, although considered inconclusive, indicated that three of these six nests had been destroyed

by coyotes, the other three by badgers. The eggs had apparently been eaten in every case. Table 8 includes the percentage of occurrence of egg shell in loess hills coyote seats and shows it rising sharply from a winter low of 2.4% to the 13.7% for spring to a summer peak of 32.1%, thence dropping steeply to 4.3% for autumn. Although all remnants of egg shell in seats were lumped under one category because of the impossibility of specifically identifying most of the fragments, and although some of the eggs represented were probably of ground nesting birds other than the pheasant, these data are provocative in this connection.

Evidence of the coyote's penchant for following row patterns, such as fence rows, field borders, and shelterbelts, was noted early in this study. Observations in the loess hills study areas in the spring of 1947 indicated that the pheasant was under some pressure from both predatory birds and mammals during the nesting season and that the row pattern of shelterbelt plantings, in which pheasants were commonly nesting, might contribute to the discovery of pheasant nests by coyotes in those situations. The significance of predation pressure by the coyote as it might relate to the annual increment of a huntable surplus of pheasants was, of course, not in any way indicated by this observation. It was suggested (Nebraska G.F.P.C. P-R. Quarterly Report, July, 1947), that if serious concern was felt at that time regarding coyote-pheasant relationships, habitat development plantings (then being accelerated in Nebraska) in some pattern other than rows might serve to reduce nest losses to coyotes, but that the effectiveness of such "psychological" barriers against predation upon nests should first be evaluated experimentally.

Any contemplation of data relative to the destruction of pheasant nests by coyotes can be made intelligently only in the light of the possibility that "predators may contribute to the prosperity and survival" of the pheasant by causing a "staggering of nesting attempts and thus preventing a catastrophic loss [of young birds] from a short period of severe spring weather" (Latham 1951).

Although the observed behavior of a predator and potential prey animals when close to each other in any given circumstance cannot be considered necessarily significant as regards their ecological relationships, such observations are interesting, perhaps provocative. At sundown (6:05 P.M.) on February 8, 1949, Fichter began watching four pheasant hens on a snow-covered north slope in the Valley County study area. They were in scanty cover, mostly sunflowers and scattered sweet clover, at about 400 yds and readily observable through 8x binoculars. They were moving about slowly and generally up slope out of a ravine which lay between them and the observer. At 6:07 a coyote, probably having watched the observer's movements for some minutes up to this time, barked and howled from somewhere in the general direction of the pheasants. There was no detectable change in the behavior of the birds, eight more of which had

walked into view by this time. At 6:11 the coyote was sighted near an old pile of baled straw and not more than 100 yd from the pheasants. The coyote shortly disappeared, trotting down the ravine out of which the pheasants had been moving. No evidence of concern was seen among the pheasants which were settling for the night at this site, the last movement among the birds being discernible at 6:40. Sign examined the following morning revealed that the coyote had left a day-time bedding site and had passed within a few yards of the pheasants as they prepared to roost. The presence of the observer standing at 400 yds might have deterred any tendency on the part of the predator to be interested in the pheasants as potential prey. The coyote did not seem disturbed by the presence of the human. At 6:30 it was in sight again, moving leisurely at less than a half-mile across open snow and across the observer's line of sight; it traversed a brushy ravine, stood on a large snowdrift where it howled twice, trotted to a low stack of alfalfa hay, climbed to the top of the stack and stood briefly silhouetted against the afterglow.

Roosting sites of pheasants were not infrequently observed on the snow during the winter of 1948-49. No evidence of capture of the birds by any predator was found on these well defined areas. Pheasants buried in snowdrifts by the severe blizzards of that winter were being detected and utilized by coyotes, however, which dug out the frozen birds from as deep as 20 to 24 in beneath the surface of the snow.

On June 11, 1948, Fichter (1950) was in a blind near a coyote den site on the Valley County study area by 4:20 A.M. Four two-minute counts of pheasant cock calls from 4:26 to 4:45 recorded a range of 83 to 104 calls with an average of 96. That number of calls is indicative of a very dense breeding population. Crowing cocks could be seen from the blind. At 5:04 the male coyote came into the denning area carrying a mature, white domestic chicken, its loosely dangling legs and neck indicating that it had been freshly killed. In getting to the farm where it caught the domestic chicken and returning to the den with it, the coyote had traveled at least 2 mi through a dispersed and spectacularly heavy breeding population of pheasants. Contemplation of the role of availability in this feeding pattern is fascinating.

#### Grouse

Because remains of the sharp-tailed grouse (*Pedioetes phasianellus*) and the pinnated grouse or prairie chicken (*Tympanuchus cupido*) in stomachs and seats of coyotes could not routinely be separated with certainty, they were tabulated simply as grouse. The somewhat comparable habits of these two species probably lends justification to this lumping as it may relate to the feeding patterns of coyotes.

According to Mohler (1950), all of the counties in the sandhills, including those with extensive sandhills south of the Platte River, plus several counties further west in the panhandle, have either prairie chickens or sharp-tailed grouse; many of these counties have

both species. Sharptails outnumber prairie chickens in the northern portion of the high plains in Nebraska and in the northwestern parts of the sandhills. Prairie chickens are more abundant than sharptails in the eastern and southern sandhills. Wintering flocks of prairie chickens move south and east out of the sandhills into the cultivated lands. Some winter movement of sharptails also occurs. Sharptails were seen in winter in the Valley County study area and prairie chickens within a few miles, both in cornfields.

Grouse was represented only in stomachs from the loess land types and the western high plains, principally in the latter (Tables 5 and 6) in which it supplied 8.4% of the total volume of contents (nearly three times as much as pheasant) and appeared in 3.1% of the stomachs. Grouse remains were not found in seats from the loess hills, but appeared in 3.6% of those from the Valentine Lakes area and in 5.9% of those from Nebraska National Forest. In each of these situations its seasonal pattern was similar to that of the pheasant, i.e., a winter high sloping gently to an autumnal low (Fig. 33).

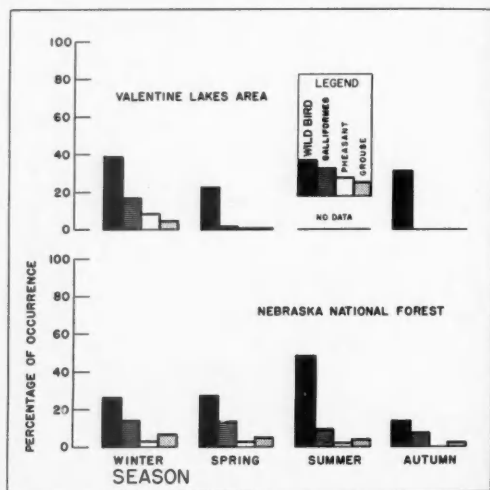


FIG. 33. Seasonal percentages of occurrence of certain avian food groups and items in 1,740 coyote seats from a xeric sandhills habitat (Nebraska National Forest) and in 419 seats from an area of lakes and marshes in the sandhills (Valentine Lakes Area).

The incidence of egg shell in seats on the Bessey Division showed slight increases through spring to a comparatively low summer peak; the relationship of this pattern to the reproductive efforts of sharp-tails in that area is, of course, unknown.

Grouse do not appear to have been of noteworthy importance in the diet of coyotes in Nebraska throughout the period of our study, even where abundant, except perhaps during the winter of 1948-49 when unusually severe storms and deep snows materially modified the coyote's feeding pattern. Table 11 presents percentages of occurrence of certain food groups and items in seats from the three segments of road

(Fig. 26 and described in the section on deer) during January, February, and March of 1948 and 1949. The percentages of occurrence of grouse remains for the latter period were from five to seven times those of the previous year, with the greatest increases occurring in seats from among the conifer plantations (A and B of Table 11). Some degree of correlation with these modifications appears in the values depicted for Galliformes in Fig. 25.

TABLE 11. Percentages of occurrence of certain food groups and items in 594 coyote seats from three arbitrary segments of the 15 mile-long graveled road on the Bessey Division of Nebraska National Forest: In 251 seats collected March 30 to April 1, 1948, and in 343 seats collected February 10 to March 3, 1949.

Food Groups and items	Road segment designation	Number of seats	LATE WINTER					
			1947-48			1948-49		
			A	B	C	A	B	C
			57	95	99	144	82	117
Mouse			45.6	68.4	47.5	33.3	59.8	76.0
<i>Microtus</i>			33.3	65.3	31.3	21.5	24.4	40.2
<i>Reithrodontomys</i>			3.5	11.6	7.1	10.4	26.8	30.8
Pocket gopher ( <i>Geomys</i> )			75.4	63.2	55.6	41.0	29.3	21.4
Rabbit			15.8	9.5	28.3	16.0	18.3	18.8
Deer			8.8	5.3	1.0	43.8	40.2	20.5
Cow			8.8	16.8	29.5	47.9	26.8	46.2
Grouse			1.8	2.1	2.0	13.9	13.4	10.2
Insect			36.8	34.7	40.4	2.1	4.9	1.7
Fruit			12.3	34.7	20.2	4.9	2.4	17.9

#### Domestic Chicken

Remains of poultry (all chicken except one turkey) were most frequent (20.9%) in stomachs from the loess plains, in which it comprised 17.9% of the total volume of food examined. No evidence of chicken was found in either stomachs or seats of sandhill coyotes (Fig. 29). Representations of chicken in 5.7% of the seats from the loess hills study areas revealed a distinct peak in the coyotes' utilization of this food item during the summer (Fig. 32).

During the course of our field work, farmers in the loess hills gave eyewitness accounts of coyotes coming boldly into farmyards to catch chickens very early on spring mornings. One farmer living near the Valley County study area, although he said he had little complaint against coyotes, explained that they do most of their damage to poultry during the summer—the chickens wander away from the farm buildings during the middle of the day and are caught by coyotes in the corn. Another landowner, living on the study area, stated that he had given up trying to raise chickens after 1947 because of the inroads coyotes had made against his flock.

The disposal of dead chickens by carrying them into fields, sometimes with loads of barnyard manure, and even by tossing them at roadsides, seems to be traditional; it has been noted by Scott (1943) as "a small but almost continuous supply of carrion chicken" for red foxes on a study area in Iowa. The relationship between this careless but time-honored practice in

Nebraska and the occurrence of chicken remains in coyote stomachs and seats is not known. We have heard the suggestion that dead hens discarded in fields offer coyotes an opportunity to acquire a liking for chicken. The problem of coyote depredations on poultry is economic and local, pinpointed at individuals flocks and probably best analyzed in relation to the pattern of poultry management in practice on each farm unit where damage is suffered.

#### COLD-BLOODED VERTEBRATES

Reptiles were well represented in coyote seats on Nebraska National Forest, very infrequently in stomachs and the other seats. These reptilian remains were largely those of lizards, although evidence that both snakes and turtles had been eaten was found. The seasonal pattern of the coyotes' light utilization of this source of food shows a peak during the summer in keeping with the phenological sequence of reptilian activity.

#### INSECTS

Insects in the diet of the coyote appear to have been more important on the basis of frequency in seats (Fig. 7) than on frequency in stomachs (Fig. 6); the statewide and year-round importance of insects to coyotes was apparently very minor volumetrically (Fig. 6). At times, however, coyotes feed exclusively on insects, and stomachs containing large numbers of such prey are spectacular; outstanding examples have been reported (Sperry 1941, Murie 1935).

Analyses of the contents of coyote stomachs indicate that insects were more important to coyotes in the high plains and sandhills than elsewhere in Nebraska, at least in winter during which season most of the stomachs were collected. It is interesting that dependence on insects for food was apparently greatest in the two land types where the average volume of stomach contents was smallest.

Seats from the study areas showed a greater frequency in insect remains in sandhills in general than in the loess hills (Fig. 10). However, the frequency in droppings from the Valentine Lakes area (Fig. 11) was about one-half that shown by loess hills seats; the highest percentages of occurrence appeared in seats taken on Nebraska National Forest. In both the dry, upland sandhill area and the loess hills (summer data lacking for the Valentine Lakes area) insect remains showed the same seasonal pattern of occurrence (Figs. 13 and 14), a slight spring build-up from a winter low, a rise to a summer peak, most pronounced in the sandhills, thence a decline to an intermediate level in the autumn. The occurrences of insect remains in summer seats in the drier sandhill situation approached that of mammalian representations, indicating a well-defined shift to insects for food during the warmer months (Fig. 14).

Coyotes apparently find grasshoppers highly palatable (Murie 1940). The presence of 345 grasshoppers and 20 crickets in the stomach of a coyote shot at about 9 P.M. on October 29, 1947, on Ne-

braska National Forest, where other foods, especially pocket gophers, were plentiful, would support this conclusion. Many species of grasshoppers winter over in nymphal stages, becoming active on warmer winter days, and thereby probably accounting for their continued albeit less frequent representations in seats through the cold months. Deep snows, and possibly other features of the severe winter of 1948-49 markedly depressed this winter pattern (Fig. 25).

The preponderance of grasshoppers (mostly Acrididae) and May beetles among the insects taken by coyotes was as notable in this as in most other studies on coyote food relationships. In addition, large numbers of a small larva, probably lepidopteran, were eaten in spring and summer on Nebraska National Forest, some seats containing up to 600 of these caterpillars.

Possible coactional relationships of insects with other food groups have been suggested in the section on major food groups.

#### FRUIT

Only wild fruits were represented in the coyote stomachs and seats examined in this study. Wild plum was most important in the loess hills seats; sand cherry and chokecherry were the most prominent fruits in those from the sandhills. Chokecherry, wild grape (*Vitis vulpina*), Russian olive, hackberry and prickly pear (*Opuntia humifusa*) were less abundantly represented, the latter two occurring only in seats gathered in sandhills.

Fruit was found in 3.6% of the stomachs but contributed only 0.8% of the total volume of contents (Fig. 6). This food source appears to have been somewhat more important on the basis of frequency in seats (Fig. 7). Occurrence in stomachs indicated that fruit was more important to coyotes in the high plains and sandhills than to those in the other land types, at least in winter, during which season most of the stomachs were secured. Data from seats, which were gathered in all seasons, show that fruit was utilized to a greater extent by loess hills coyotes than by those in the sandhills (Fig. 10), and within the latter type, more by those in the drier area (Fig. 11).

The seasonal pattern of fruit consumption shows the greatest fluctuation of that of any food group. In all study areas the summer to autumn increase was outstanding, the shift from zero to 95.6% of occurrence in the loess hills being the most pronounced. Seats composed exclusively of the remains of fruit, mostly seeds (pits), were not uncommon in season, with numbers of seeds ranging up to 45 for wild plum, 300 for hackberry, 520 for chokecherry, and 750 for sand cherry. The higher winter frequency in loess hills seats, as compared with the winter values in seats from sandhills, reflects the persistence of dried wild plums on the ground until late in the winter.

#### GRASS

While grass has been considered a food item of the coyote by Murie (1935), the apparently undigested condition of grass in seats seen in this study leads us

to concur with Sperry (1941) who could detect no evidence that grass served the coyote as a food in the true sense, although he found evidence of a "sudden and short-lived" but unexplainable "craving for grass" in June. A comparable seasonal pattern was apparent in the seats of coyotes in Nebraska. A few early summer seats were nearly 100% green grass.

#### DISCUSSION

Murie (1945) has summarized the feeding habits of the coyote by saying, in part, that the predator usually "seeks an abundant animal form, whose habits are such that it lends itself to easy capture on a scale large enough to furnish a staple food supply." Cottontails, jack rabbits, meadow mice, pocket gophers, muskrats, cattle, pheasants, and domestic chickens variously afforded such staple supplies of food for coyotes in Nebraska during the period of this study. The broad outlines of this pattern are not new; some of the local variations and their seasonal shifts may furnish new, or at least corroborative information.

The economic aspects of coyote predation are not within the province of this discussion. Suffice it to say that the coyote has long been without question looked upon as an economic liability in Nebraska and has been summarily dealt with as such, often ineffectively and uneconomically, and always without knowledge of or concern for all possible biological consequences in the wild community.

Operations directed at the coyote in the name of wildlife management have, likewise, not always been concerned with total effects. So-called "control" measures have been called for and carried on against the coyote as an alleged mechanism for increasing game bird populations without regard for or attempt to determine the pattern of even the ostensibly desired results, to say nothing of compensatory results that may have influences upon the desirable prey species more deleterious than the original pressure of predation. Only experimentation can measure such effects, and only measurement can eliminate unsound and expensive guesswork.

Because the "net effect of predation upon a particular prey species" is not measured "in terms of its per cent occurrence in the predator's diet" (Latham 1951), discussion of our findings is significant only in relation to further and experimental studies. It has been shown that rabbits, meadow mice, pocket gophers, muskrats, and pheasants were the wild vertebrate food items variously prominent in the coyote's feeding pattern in Nebraska. There is no shred of evidence in the data published here on which to base a conclusion that the populations of any of these prey species was or was not effected by its relationship with the coyote. Our data might, however, be of service in pointing out or reiterating the following:

1. Coyote feeding patterns vary from locality to locality, from season to season, from year to year; lumping of data can obscure possibly important



local patterns and generalizations can be misleading.

2. Further investigations should gather detailed population data on all potential prey species wherever and during whatever period feeding patterns are studied.
3. At least three species must be used as "yardsticks" in measuring the populational effects of experimentally depressed populations of the coyote.
4. A method for securing reliable indices of coyote population densities must be sought.
5. The nature of the coyote's hunting territory with its possible seasonal variations must be known.

Three possibilities take precedence in any consideration of further studies on coyotes as depressants of pheasant populations in Nebraska, or elsewhere:

1. That compensatory mechanisms exist in wild populations that may be more decisive than the force of predation in determining animal densities.
2. That annual under-harvesting of pheasants by hunters may obviate the necessity of concern over the fate of the bird's populations in response to predation by coyotes.
3. That the function of availability suggests a more constructive approach to the coyote-pheasant problem, be it real, imagined, or only alleged.

Availability of a prey species to a predator is largely a function of its numbers per unit area, its habits, and certain factors of the habitat, all operating in an intricate pattern of interrelationship that varies from place to place and from time to time. As a rule, greater numbers of a prey species probably result in increased availability, whether absolutely or in relation to factors of security in the habitat. Habits, such as rhythmic behavior, in part responsible for "the difference in the relative proportions of white-footed mice and meadow mice in the diet of the red fox" (Scott 1945) for example, are fixed by inheritance. On the other hand, factors of the habitat are subject to considerable variability and to manipulation.

More and more pheasants are apparently wanted by sportsmen. Their habits cannot be appreciably altered. If increased protection of greater numbers of birds from predation is wanted, the habitat may be made to provide it. Twenty years ago, Errington (1935) urged that "enlightened and truly effective predator control should attempt far more than at present to make game . . . difficult for predators to get rather than attempt great reductions in numbers" of the predatory species. Comprehension of the functions of habitat in shaping the pliable feeding pattern of the coyote can point the way to a constructive, natural control of predation upon the pheasant, if control is needed.

Evidence that the pheasant was an important food item of coyotes in the loess land types is not categorical cause for alarm nor basis for launching any of the popular forms of control against these predators.

It is, on the contrary, cause for rejoicing. That coyotes were numerous in the best pheasant range, and may still be, is not news. If predation is "essentially a by-product of population rather than a broadly dominant influence on population" (Errington 1937), and it seems to be, the degree of predation upon pheasants by coyotes in the loess land types, as revealed by our data, is an indicator that the populations of birds desired by sportsmen were there to be harvested.

### SUMMARY

Declines in pheasant populations in Nebraska during the middle 1940's were attributed by many sportsmen to predation by the coyote which was abundant. A study, planned in distinct but dove-tailed exploratory and experimental phases, was undertaken to gather biotic data by which to judge the justifiability of spending sportsmen's dollars in control of coyotes. Only the exploratory phase of the investigation materialized.

Field observations were conducted from February, 1947 to March 1952. Stomachs and seats of coyotes were collected from February, 1947 until late in March, 1951.

Analyses of 2,500 seats and of the contents of 747 stomachs were made. Findings are expressed as percentages of occurrence (frequency) in stomachs and seats, and as percentages of volume in stomachs.

Data furnished by extensively secured stomachs are categorized on the basis of the five generalized major land types in the state, namely, western high plains, sandhills, loess hills, loess plains, and drift hills.

Relatively intensive collecting of seats and observations on coyote behavior were accomplished on four study areas—two with different water relations in the sandhills, namely, the Bessey Division of Nebraska National Forest in Thomas and Blaine counties, and the Valentine Lakes area in Cherry County, and two essentially like areas in the loess hills of Valley and Greeley counties.

Four major food groups—mammal, bird, insect, and fruit—in that order of decreasing quantitative importance comprised the basic feeding pattern of the coyote. This pattern was subject to areal and chronological modifications.

The mammalian food group was consistently dominant in the feeding pattern; the degree of the coyote's dependence upon birds, insects, and fruit (especially the latter two) was so variable that marked shifts in the representations of these groups were characteristic of the basic pattern. An enormous autumnal increase in the utilization of fruit was the most striking seasonal trend. Insects became important in summer.

Coyotes relied upon small wild mammals, principally rabbits, mice, and pocket gophers, for the great preponderance of their food.

Rabbits (cottontails and jack rabbits) furnished the preponderance of food in the loess land types and the drift hills, especially in the latter where cot-

tontails were abundant. Seasonal utilization of rabbit showed strikingly different local patterns. Notable recent increases in cottontails in the older cedar plantations on Nebraska National Forest, where cottontails have heretofore been scarce, coincident with "1080" operations against coyotes on surrounding lands demand study.

Mice were eaten often by coyotes, most importantly in the high plains and sandhills. All patterns of mouse utilization are largely functions of the consumption of meadow mice, which provided a staple food supply for the coyote. The frequency of their remains surpassed that of rabbit in some situations. Meadow mouse was the most frequently represented food item in seats from the Valentine Lakes area where an autumnal peak was outstanding.

A seeming abundance of kangaroo rats on Nebraska National Forest was not reflected in coyote seats, suggesting contemplation of availability and predilection.

The pocket gopher was represented in stomachs from all land types, but ranked first in the diet of coyotes only on Nebraska National Forest where it was also under pressure of "control" operations employing poison, the Forest Service considering its populations at dangerous densities in many of the coniferous plantations. Estimates made in this paper indicate that coyotes might have eaten an annual average of 4.3 pocket gophers per acre on the Bessey Division where they exerted their heaviest pressure on gophers in the spring.

Remains of muskrat were found in stomachs and seats from sandhills only. This furbearer ranked second only to meadow mouse in the coyote's menu in the Valentine Lakes area, reciprocal utilization of the two prey animals being evident. The degree of coyote predation upon muskrat is probably a function of emergency conditions to which a muskrat population in any instance is being subjected.

Mule deer became an important food item for coyotes in Nebraska National Forest during the unusually severe winter of 1948-49. The percentage of coyote-kills, in relation to death of deer by other causes in this situation, is not known.

Cattle as a source of food were most important to coyotes in the sandhills. Although calves are reportedly killed by coyotes, most occurrences of cow remains in seats and stomachs probably represent carrion. The carcass of one cow was known to furnish identifiable remains for coyote seats for at least nine months, possibly longer.

Apparently coyotes rarely hunt small bird prey in a systematic manner. A summer peak in small bird remains in seats appears to reflect increased availability of ground-nesting species taken advantage of only accidentally by the coyote.

The pheasant provided an important food item for coyotes in loess hills and plains. An expected spring peak in utilization because of supposedly increased vulnerability of hens on nests did not develop. Some early nests appeared to have been destroyed by coy-

otes, possibly due to conditions of the nesting cover.

Grouse were not noteworthy in the diet of the coyote except during the severe winter of 1948-49.

Heaviest use of domestic chicken occurred in the loess land types, especially in summer, a problem probably best considered in relation to poultry management practices.

The coyotes' generally light use of cold-blooded vertebrates, principally lizards, showed a slight summer peak, especially in the sandhills.

Grasshoppers, May beetles, and a probable lepidopteran larva appeared prominently in the summer diet of coyotes. Such a trend may serve to slightly release pressure on some vertebrate prey species.

Wild fruit, principally chokecherry, sand cherry, and wild plum, was eaten in surprising quantities in summer and autumn, particularly the latter, and may have partially supplanted prey animals in the coyote's diet for brief periods.

Grass was eaten intentionally, especially in summer, but apparently was not digested.

Data presented in this report furnish no measurements of net effects of predation on any prey species; they are significant only in relation to further and experimental studies.

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# VEGETATIONAL CHANGES IN THE SAN ANTONIO PRAIRIE ASSOCIATED WITH GRAZING, RETIREMENT FROM GRAZING AND ABANDONMENT FROM CULTIVATION

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## TABLE OF CONTENTS

	PAGE		PAGE
INTRODUCTION .....	39	Vegetational Retrogression in Relation to Micro-	
HISTORY OF AREA .....	40	topography .....	48
REVIEW OF LITERATURE .....	41	Secondary Plant Succession on Land Retired from	
Vegetation .....	41	Grazing .....	50
Succession .....	42	Secondary Plant Succession on Abandoned	
DESCRIPTION OF AREA .....	42	Cultivated Land .....	51
Geology .....	42	Seasonal Development of the Vegetation .....	54
Soils .....	42	Early spring aspect .....	54
Climate .....	42	Spring aspect .....	54
METHODS .....	43	Summer aspect .....	54
RESULTS AND DISCUSSION .....	43	Fall aspect .....	55
Climax Vegetation .....	43	Winter aspect .....	55
Vegetational Retrogression Caused by Grazing ...	44	SUMMARY AND CONCLUSIONS .....	55
Increase in Density of Mesquite .....	47	LITERATURE CITED .....	57
Effects of Moderate Grazing on Hay Meadows ....	48		

## INTRODUCTION

The San Antonio Prairie as represented in Figure 1, is located in southeast-central Texas. The prairie is about 100 mi. long and ranges between 1 and 6 mi. in width. The boundaries are irregular and the area appears as a broken belt of grassland. The larger discontinuities are caused by the major rivers which flow through the general region in a southeasterly direction. The vegetation bordering the larger streams and their tributaries is woodland composed principally of species of *Quercus*, *Celtis* and *Ulmus*.

The San Antonio Prairie is completely surrounded by oak-hickory forest and is one of several small prairies appearing in this woodland matrix. The Blackland Prairie lies to the north and the Fayette Prairie to the south.

Much of the land within the San Antonio Prairie is used for a variety of agricultural crops, principal-

ly cotton, corn and small grains. Many sites which have not been cultivated have been grazed by domestic livestock, or used consistently since settlement for native hay production.

Most of the grazed pastures are relatively small in size. The general practice is to graze small dairy herds yearlong without pasture deferment or rotation. This practice is altered on some ranches where beef herds constitute the major enterprise. Supplemental feeding of concentrates is practiced in some instances during the dry-feed season, which results in more uniform use of all the vegetation. Certain areas are grazed during part of the year and are deferred the remainder of the time.

This diversity of land use has introduced many changes in the native vegetation making it quite variable in character. Tall grasses are most apparent in the hay meadows and similar areas that have received relatively light use. The grazed pastures



FIG. 1. Map showing location of the San Antonio Prairie and the areas of mesquite within its boundaries.

support a growth of shorter grasses. The tall grasses do not occur to any great extent in the heavily used pastures. Numerous fields which were normally cultivated each year have subsequently been abandoned and the vegetation allowed to re-establish itself through natural means. The abandoned fields support many different combinations of species ranging from broadleaved forbs to tall grasses. Noxious brush, composed mainly of mesquite, occurs in mature stands in many of the grazed pastures and along the road-sides.

A knowledge of the changes in the vegetation in relation to grazing and cultural uses is of interest from an ecological point of view and is fundamental in the practice of efficient land use of these and similar areas.

Studies were conducted in the San Antonio Prairie during 1950 and 1951 for the following purposes: (1) to determine the nature of climax vegetation and the pattern of vegetational change associated with various degrees of livestock grazing; (2) to ascertain the characteristics of range improvement following the removal of grazing animals from deteriorated pastures; and (3) to determine the stages of secondary plant succession on areas abandoned from cultivation.

The author wishes to express appreciation to the many persons who assisted in this study. Dr. Harold F. Heady, School of Forestry, University of California, suggested the study and gave helpful advice

during the investigation. Drs. Vernon A. Young, Omer E. Sperry and Robert A. Darrow, Department of Range and Forestry, Agricultural and Mechanical College of Texas, gave valuable assistance in the preparation of the manuscript. The writer also expresses gratitude to his wife, Marian D. Launchbaugh, for her aid in collecting and compiling the field data.

#### HISTORY OF AREA

Prior to the arrival of European settlers, the area comprising the San Antonio Prairie was inhabited by members of the Keechi and Kickapoo Indian tribes (Wood 1901). The Wacos, the Tewakanos, the Tonkawas and Comanches made raids upon the early settlers of this particular section of Texas (St. Clair 1931). No doubt most of these tribes frequented the area prior to settlement in search of wild game. Wood (1901) stated that the Keechi tribe practiced some cultivation in certain sections of the fertile prairie.

The Old San Antonio Road running through the prairie played a major role in the settlement of the area. It has been traveled by the Spanish, French and Americans for more than 400 years (Norvell 1945). In early days it was simply a trail for pack mules. The Spanish, who located this road from San Antonio to Nacogdoches, selected the best crossings on the streams and the most desirable ground, avoided the hills and sandy stretches, and at the same time minimized distance. Thus the road was laid out over firm prairie soil (Wood 1901).

The movement for the colonization of this portion of Texas began when Moses Austin applied to the Spanish authorities at San Antonio de Bexar in 1820 for approval to settle some families in Texas (Barker 1925). Several pioneers moved into the area shortly after that date. W. B. DeWees, who came to a point within the present boundary of Brazos County and near the junction of the Old San Antonio Road and the Brazos River on January 1, 1822, wrote to a friend in Kentucky on July 16 of that year of the prairies in the vicinity, and of the abundant wildlife and cattle found grazing there (DeWees 1852).

Bailey (1905), reported that buffalo once ranged over the entire state of Texas, and were very numerous in the prairies of the eastern part of the state.

Rock & Smith (1878), indicated that the prairie had about its present proportions and that stocking was heavy, approximately 5 acres were allowed per animal unit yearlong.

The early settlers of Brazos county grew various food crops for home use and raised livestock on the extensive pasture and open range as a source of income. With the advent of railroads and the development of markets, the lands were rapidly fenced and divided into farms, so that by 1914 there were no farms or ranches devoted to cattle raising exclusively, although considerable land unfavorably located for, or poorly adapted to, cultivated crops was fenced and utilized for pasture (Veatch & Waldrop 1914). These

authors stated also that the prairies supported a large variety of grasses, and that it was a common opinion that unpalatable weeds were increasing and greatly reducing the value of the uncultivated lands for grazing.

At present a large proportion of the cultivated land in southeastern Texas is found in the San Antonio and similar interior prairies. About 50% of the study area is in cultivation (Bonnen & Thibodeaux 1937). The pasture land is used primarily for cattle ranching and the livestock production on farms is largely for home consumption.

## REVIEW OF LITERATURE

### VEGETATION

The San Antonio Prairie has been treated in several general vegetational classifications, which vary in the designation of plant associations and major dominants of the area. Tharp (1926) stated that the Grassland Formation in Texas is represented by the *Andropogon-Stipa* association with dominants of silver beardgrass (*Andropogon saccharoides*),<sup>1</sup> little bluestem (*A. scoparius*), big bluestem (*A. gerardi*), and Texas wintergrass (*Stipa leucotricha*). The northeastern part of the association is separated from the southeastern part by the Deciduous Forest which occurs as a broad belt with occasional local areas of *Andropogon-Stipa*; such as the San Antonio Prairie.

Most of the area east of the 98th meridian in Texas was placed in the Coastal Prairie by Weaver & Clements (1938), and Clements & Shelford (1939), with Texas wintergrass and silver beardgrass indicated as the major dominants. The central portion of the Coastal Prairie which includes the San Antonio Prairie was referred to by these investigators as an area of mesquite alternates and bands of post-climax woodland of oak-hickory; the former found regularly on hard soil or black land and the latter on sandy areas.

Blackland prairie of Walker County, Texas, which lies partly in the broad belt of Deciduous Forest, is similar to that of the counties in the Blackland Prairie Belt to the west and was considered to be an association of *Stipa*, *Sporobolus* and *Andropogon* (Warner 1942). The indicated dominants are silver beardgrass, big bluestem, tall dropseed (*Sporobolus asper*) and Texas wintergrass. However, results of a study in blackland prairie in Brazos County, Texas, by Timmons (1942) differed somewhat. These two authors agreed on the association represented in the two counties but Timmons found big bluestem, little bluestem, Texas wintergrass, tall dropseed and side-oats grama (*Bouteloua curtipendula*) to be the important dominants.

Carpenter (1940) placed the Blackland Prairie in the southern faciation of the Tall-grass Prairie (*Andropogon-Bison-Canis* association). Quack grass (*Agropyron repens*), blue grama (*Bouteloua gracilis*), side-oats grama and little bluestem are the binding

dominants of the association with the addition of Texas wintergrass, silver beardgrass, slender bluestem (*Andropogon tener*) and splitbeard bluestem (*A. ternarius*) in high prairie; silver beardgrass and few-flowered panic-grass (*Panicum oligosanthos*) in sloping prairie; and big bluestem in low prairie.

Dyksterhuis (1946) considered that the Fort Worth Prairie, which has been included in the associations of several of the authors cited above, is a part of the True Prairie association. Over the climax portion the principal dominant is little bluestem, while Texas wintergrass and silver beardgrass are the major dominants in the grazing disclimax. The observations of Bruner (1931) on True Prairie, which is separated from the Fort Worth Prairie only by the Red River, agree with this. Bruner stated that the True Prairie of Oklahoma is characterized by a little bluestem con-sociation, with silver beardgrass second in importance.

The San Antonio Prairie and the small prairies located in the broad Deciduous Forest belt of East Texas have been referred to as "mesquite flat" country (Jonson 1931). Mesquite (*Prosopis juliflora* var. *grandulosa* (Torr.) Cockerell) occurs throughout the Prairie at the present time; however, there is some indication that this woody plant has increased in abundance since settlement.

Malin (1953) concluded from early accounts of mesquite range, density and tree size in the southwest, that the present geographic range of distribution is about the same as it was at the opening of the 19th century. The quantity of mesquite during the middle of the 19th century was substantial. Trees occupied the drier sites as well as stream banks. The important changes have been in the growth form and increase in density of the trees. The transition has been from savannah to dense jungle-like stands.

Although incompletely known, the principal range of mesquite in Texas was set by Captain Marcy in 1854 as between 26° and 36° north latitude, and between 97° and 103° west longitude (Parker 1856). This range would include roughly the southwestern half of the San Antonio Prairie.

According to Bailey (1905), the 1905 range of greatest mesquite density in Texas was west of the boundary set by Captain Marcy and did not include the San Antonio Prairie. The 98th meridian marked the eastern extension in the north-central section of the state. Bailey stated further that a few outlying mesquite trees were found east of this line.

Another writer expressed the opinion that early travelers of the Old San Antonio Road were responsible for the spread and increase of mesquite eastward. These early travelers carried mesquite beans as supplementary feed for their pack animals when traveling northeastward, thus spreading viable seeds along the way (Norvell 1945).

Overgrazing by domestic animals, extensive cultivation and suppression of periodic prairie fires have been cited as positive factors in encouraging the spread and increase of mesquite in the prairies of Texas. These observations were made by Smith as

<sup>1</sup> Nomenclature for grasses follows Hitchcock (1950); for other species, Reeves & Bain (1946) unless authorities are given. Common names are from Kelsey & Dayton (1942).

early as 1899. Bray (1906) and Cook (1908) reported similar conclusions a few years later.

The postclimax woodlands of savannah-like character occupying the sandy area surrounding the San Antonio Prairie are characterized by post oak (*Quercus stellata*) and blackjack oak (*Q. marilandica*) as the important dominants with splitbeard bluestem, broomsedge bluestem (*Andropogon virginicus*), little bluestem, big bluestem and Florida paspalum (*Paspalum floridanum*) being the important grasses of the understory vegetation (Warner 1942). This woodland area is very similar to the Eastern and Western Cross Timbers which were regarded by Weaver & Clements (1938) and Dyksterhuis (1948) as oak savannah in which the grasses are climax dominants. The oaks were considered subclimax, and little bluestem was considered the main dominant, with Indian grass (*Sorghastrum nutans*) and big bluestem as lesser dominants.

#### SUCCESION

Plant succession in the midwestern prairies has been studied by Smith (1940b) and Weaver & Hansen (1941). Riegel (1944) presented the pattern of succession in the mixed-grass type of Kansas and referred to several additional studies of natural succession in the central and western Great Plains Region.

Tharp (1926) in a brief discussion of succession in the Blackland Prairie of Texas pointed out that three rather general stages are represented on abandoned cultivated land.

Five stages of succession following cultivation or heavy grazing have been recognized in the blackland prairie vegetation of Brazos County, Texas (Timmons 1942). They are: (1) an annual weed and grass stage; (2) a perennial and annual weed and grass stage; (3) a subclimax stage of subdominants; (4) the climax stage of perennial grasses; and (5) a postclimax stage of woody species in certain areas. Warner (1942) listed only four stages of succession on a similar prairie type in Walker County, Texas.

Plant succession on sandy land similar to that bordering the San Antonio Prairie has been described by Trew (1948) and Warner (1942), in Brazos and Walker Counties respectively, and by Dyksterhuis (1948) in the Western Cross Timbers.

The trends in succession of the important grasses and forbs under progressively less disturbance by grazing in the Fort Worth Prairie have been reported by Dyksterhuis (1946). The prairie species were grouped in the three following categories depending upon their behavior in the subere: (1) species that increase in relative coverage; (2) species that decrease some in relative coverage after a period of increase; and (3) species that are ultimately eliminated.

Daubenmire (1940) listed the plants which increase, those which decrease, and those which invade under grazing pressure in the Agropyron bunchgrass prairie of southeastern Washington. Weaver & Hansen (1941) and Smith (1940a) give similar information

for the prairie of Nebraska and Mixed-grass Prairie of Oklahoma, respectively.

#### DESCRIPTION OF AREA

##### GEOLOGY

Sellards, *et al.* (1932), in a description of the geology of Texas, showed that the soils of the San Antonio Prairie developed from sediments of the Claiborne group of the Eocene age. The parent materials came from outcrops of soft clays and unconsolidated, fine-grained sands of the Crockett formation. The area is part of a constructional plain, the underlying sediments having been elevated above sea level, so that the old deposition surface forms the present land surface (Veatch & Waldrop 1914). Stream erosion has modified the plain since its elevation, but a complete drainage system has not yet been developed. There is no deep stream cutting or topographic relief, and the region is still in a state of topographic youth.

The average elevation of the area is 315 ft. above sea level. The rolling nature of the topography causes a variation of 75 ft. from the mean in many places.

##### SOILS

The soils of the San Antonio Prairie have been classified as belonging to the Wilson and the Crockett series, the two having very irregular boundaries and lying intermingled throughout the prairie (Carter 1931; Veatch & Waldrop 1914; Bennett 1907; Winston, *et al.* 1907; Burgess & Lyman 1905). The topsoils of both series vary from 8 to 15 in. in depth, and are black to dark-gray in color. Although the topsoils are non-calcareous, they grade below into clay subsoil which often contains a small amount of calcium carbonate. The Wilson series differs in color from the Crockett in that black or dark drab is the predominating color in the subsoil, while red is characteristic of the Crockett subsoils. Otherwise they have very similar properties.

##### CLIMATE

The climate of the San Antonio Prairie is subhumid in character and is marked by a relatively long growing season, erratic precipitation, high temperatures, high humidities, and relatively high wind velocities (U. S. Dept. of Commerce 1949, 1950; Norquest 1941). The winters are generally very mild with little or no snow fall being recorded. Sleet storms occur occasionally.

The average growing season includes about 258 days. The last spring freeze occurs between March 8 and March 10, while the first fall freeze comes between November 18 and November 27.

Rainfall records taken at three stations show that the average annual precipitation varies from 45.21 in. at Madisonville near the north end of the prairie to 38.94 in. at College Station near the central portion, to 37.42 in. at Smithville at the southern end of the prairie.

The average annual precipitation is fairly evenly



distributed over the region each month. The departures of monthly precipitation from the mean were very high during 1949 and 1950. The total rainfall at all stations was nearly 9 in. above the mean in 1949. The fall of 1950 was one of extreme drought at all three stations.

The mean monthly temperature ranges between 51° F in January and 84° F in August at College Station. The readings at this location are typical of the entire prairie. Annual evaporation at College Station is 57.0 in., 18.03 in. in excess of the mean annual precipitation (Karper 1933). The average relative humidity at the central weather station varies between 74.9% in August and 80.0% in January, with an average of 77.2% annually. Wind movement at College Station averages 3,421 mi. per month and is greatest during the winter and spring months.

### METHODS

Three sampling procedures were employed in the vegetational analyses of fields having various histories of past use. In all instances fields are compared on the basis of average values obtained from a number of randomly located plots. Stratified sampling was deemed necessary only in fields which had obvious differences in vegetation associated with differences in topographical features. In fields which did not exhibit such differences the sampling was completely randomized. Nearly all of these fields were less than 100 acres in area, thus it was assumed that the complex of factors influencing the vegetation, e.g., climatic, edaphic and biotic, was nearly uniform throughout each field.

Twenty-three fields representing different stages of vegetational succession and retrogression were selected for intensive study. The following classification is a list of types of areas sampled:

- A. Hay meadows
  - 1. Ungrazed
  - 2. Grazed
- B. Grazed pastures not used for hay production
- C. Abandoned cultivated land
  - 1. Ungrazed
  - 2. Grazed

Basal density and percentage composition of the vegetation were determined on all the fields sampled by using a one-meter steel rod, 3/16-in. in diameter, graduated in centimeters as a modification of the line-interception method of sampling range vegetation as described by Canfield (1941). Each of the fields was sampled with 30 line transects, 5 m in length.<sup>2</sup> The sample thus obtained consisted of a list of grasses and forbs intercepted at ground level and the distance to the nearest 0.1 cm along each line which

was in contact with each species. Basal density was computed from these measurements by dividing the length of line touched by each species by the total transect length and expressed in percent. Basal density may be defined as the amount of soil surface actually occupied by the basal portion of living plant material expressed in units of area or percentage of area.

To compare fields in relative terms, the composition of the vegetation was derived from the line transect measurements by dividing the length of line in contact with each species by the total length of line touching vegetation and expressed in percent. The percentage value for each species shall be referred to as percentage composition. In this study percentage composition is quantitative and expresses the relative proportion of plant species present from basal area measurements.

The second sampling procedure consisted of counting the broadleaved herbs in each field on 30 randomly located belt transects which were 5 m in length and 5 cm wide. Following the forb counts the width of each belt transect was extended to 1 m in fields containing mesquite in order to determine basal area and stem counts of the trees.

Thirty 100-foot line transects were used as the third sampling procedure in fields containing mesquite to determine percentage crown density. The lines were distributed at random in each field and the amount of each line directly beneath mesquite crowns was recorded to the nearest 0.5 ft. Crown density was determined by dividing the length of line under crowns by the total transect length and expressed in percent. This density figure gives the percentage of area beneath mesquite crowns in the sampled fields.

### RESULTS AND DISCUSSION

#### CLIMAX VEGETATION

An extensive survey of the San Antonio Prairie revealed that hay meadows and cemeteries which are not grazed by domestic livestock are the most suitable areas for determining the nature of climax vegetation. Mowing apparently has had little influence upon the composition of the herbaceous vegetation of the prairie. Most meadows are mowed annually during late June or early July. This time of cutting not only allows most of the vegetation to develop beyond the critical early spring growth period but is prior to seedstalk formation of the major grasses so that after the removal of the hay crop the plants are able to make new growth and complete their life cycles.

Many of the hay meadows of this prairie have been restricted entirely to native hay production for over 50 years. These meadows have never been cultivated, hence their soils have not been altered by tillage.

The responses of certain perennial forbs furnish evidence that near-climax conditions have been maintained under mowing. Although many forbs complete their flowering and seed-producing stages prior to mowing, several perennial composites flower in the fall. Observations before and after cutting indicated

<sup>2</sup> Line-interception measurements on 20 ten-meter lines were taken in a preliminary study during 1950 in a hay meadow to determine the number and length of lines to use. The standard deviation "s" and the mean " $\bar{x}$ " of the basal density of the major species were calculated and the following formula used to find the number (Snedecor 1948):

$$N = (100)^2 t^2 / p^2 \bar{x}^2$$

Values for "t" and probability "p" were chosen at the one and 10% levels respectively. Results of this preliminary study indicated that 30 line transects, 5 m in length, were sufficient when the number was based on basal density of the important species.

that fall-flowering species recovered from mowing and completed their life cycles. Mowing removes the top growth only once during the year, grazing animals on the other hand are more selective and may remove the above ground portions of the same plants several times a season.

It was apparent that railroad right-of-ways and road sides either had soil disturbances or are grazed frequently by domestic livestock allowed to run free; also, because of the value of the San Antonio Prairie for agriculture and grazing, no large areas were found which had not been disturbed by mowing, grazing or cultivation. Thus areas which have not been tilled and are subjected only to annual mowing were considered to have the best representation of climax vegetation.

Three hay meadows and one cemetery which had not been grazed by domestic livestock for over 50 years were used for intensive study of the climax. The percentage composition and density data obtained on these four areas are presented in Table 1.

TABLE 1. Relative importance of species in ungrazed relict areas.

Treatment.....	MCWED - UNGRAZED				
Field Number.....	1	2	3	4	Average
<i>Species that Decrease</i>					
	Composition (Percent)				
<i>Andropogon scoparius</i> .....	76.9	72.0	71.3	69.3	72.4
<i>Bouteloua curtipendula</i> .....	4.4	10.4	7.3	5.7	7.0
<i>Andropogon gerardi</i> .....	2.0	2.4	0.7	...	1.3
<i>Sporobolus asper</i> v. <i>pilosus</i> .....	2.0	...	0.2	2.0	1.0
<i>Sorghastrum nutans</i> .....	1.8	2.3	2.7	3.8	2.6
<i>Paspalum floridanum</i> .....	0.4	0.3	0.1	...	0.2
<i>Andropogon ellipticus</i> .....	0.2	0.3	...	0.2	0.2
<i>Festuca octoflora</i> .....	0.1	0.2	...	0.1	0.1
Forbs.....	3.1	2.6	3.1	3.2	3.0
Total.....	90.9	90.5	85.4	84.3	87.8
Basal Density (Percent).....	4.0	5.2	3.7	4.0	4.2
<i>Species that Increase</i>					
<i>Bouteloua rigidula</i> .....	4.6	3.0	8.2	3.6	4.8
<i>Stipa leucotricha</i> .....	1.3	0.6	0.7	2.4	1.2
<i>Aristida</i> spp. (annual).....	0.9	0.3	0.8	3.0	1.2
<i>Sporobolus asper</i> .....	0.7	1.2	1.3	4.1	1.8
<i>Andropogon saccharoides</i> .....	0.5	0.1	T	...	0.1
<i>Bouteloua hirsuta</i> .....	0.3	1.7	2.6	0.9	1.4
<i>Paspalum plicatulum</i> .....	0.3	1.5	...	...	0.5
<i>Panicum</i> spp. (perennial).....	0.1	0.7	0.2	0.8	0.5
<i>Manisuris cylindrica</i> .....	...	T	0.2	0.4	0.2
Forbs.....	0.4	0.4	0.6	0.5	0.5
Total.....	9.1	9.5	14.6	15.7	12.2
Basal Density (Percent).....	0.4	0.6	0.6	0.7	0.6
Total Basal Density.....	4.4	5.8	4.3	4.7	4.8

An analysis of variance indicated that there is no significant difference between these fields with respect to basal density and composition.

The plants were divided into three categories depending upon their reaction to grazing. Species that decrease are those that showed a lower percentage composition with an increase in stocking rate. Those plants which tended to increase in percentage under

grazing are termed increasers. The plants that established themselves for the first time in grazed pastures are called invaders.

Little bluestem, a decreaser which made up an average of 72.4% of the total composition, was the most important species found in the relict areas. Decreasers constituted 87.8% of the vegetation while the increasers comprised the remaining 12.2%. Texas grama (4.8%) was the most important increaser.

The decreasers had a basal density of 4.2% while the increasers showed a 0.6% basal density.

The outstanding feature of the data presented for the relict areas is the extreme importance of little bluestem as a climax dominant. Observation of all relicts visited confirmed this finding. Side-oats grama comprised 7.0% of the composition. This relatively low percentage classed it as a dominant of secondary importance along with Indian grass, Texas grama, big bluestem and hairy tall dropseed (*Sporobolus asper* var. *pilosus*). Figure 2 is a view typical of all the hay meadows. The gently rolling topography which is characteristic of the prairie is illustrated as well as the high foliar density<sup>3</sup> which reached approximately 100% at maximum vegetative development. Even though the foliar density may be sufficiently high to completely shade the surface of the soil, the basal density never exceeded 5.8%.



FIG. 2. An ungrazed hay meadow (Field 4) typical of climax vegetation. Little bluestem is the most important species.

#### VEGETATIONAL RETROGRESSION CAUSED BY GRAZING

After determining the best development of vegetation possible under existing conditions in the prairie, it is possible to consider the responses of the plants to various intensities of utilization by livestock. Nine pastures subjected to different stocking rates were studied and the data are shown in Table II. Data on stocking rates supplied by the owners are average values which have been maintained for more than 15 years on each field. Field 5 has been used for hay production and grazed from August to May during favorable years at the rate of 0.7 A per animal unit per month.

<sup>3</sup> Expresses percentage of soil surface completely shaded by foliage, in contrast to basal density which refers only to the basal growth of the vegetation.

TABLE 2. Composition and basal density of the important grasses and forbs as related to various intensities of utilization on native hay meadows and pastures.

Field Number.....	5 <sup>1</sup>	6	7	8	9	10	11	12	13
Stocking Rate (Acres/AUM) <sup>2</sup> ...	0.70	1.25	0.61	0.50	0.33	0.31	0.20	0.14	0.12
<i>Species that Decrease</i>									
<i>Andropogon scoparius</i> .....	55.2	29.5	13.6	1.4	...	0.2	0.7	...	...
<i>Bouteloua curtipendula</i> .....	6.6	4.3	4.7	2.1	2.0	1.3	1.3	0.5	...
<i>Andropogon gerardi</i> .....	0.2	0.3	...	0.3	...	...	...	...	...
<i>Sporobolus asper</i> v. <i>pilosus</i> .....	1.2	0.1	1.0	...	...	0.1	...	...	1.1
<i>Sorghastrum nutans</i> .....	1.6	0.8	0.4	...	...	...	...	...	...
Other grasses <sup>3</sup> .....	...	0.6	...	0.1	...	...	...	...	...
Forbs.....	3.7	4.3	0.6	0.8	0.5	0.1	0.1	0.1	1.5
Total.....	68.5	39.9	20.3	4.7	2.5	1.7	2.1	0.6	2.6
Basal Density (Percent).....	2.7	1.6	1.8	0.2	0.1	0.1	0.1	T	T
<i>Species that Increase</i>									
<i>Bouteloua rigidisetula</i> .....	17.5	21.6	61.2	51.1	35.3	25.3	32.9	35.6	13.4
<i>Stipa leucotricha</i> .....	1.8	5.1	5.7	14.7	22.0	44.8	36.2	32.3	33.2
<i>Aristida</i> spp. (annual).....	0.2	0.7	0.7	0.8	1.8	0.6	1.0	2.8	6.6
<i>Sporobolus</i> spp. (annual).....	1.9	1.5	3.0	3.0	4.2	4.6	1.2	1.2	0.3
<i>Andropogon saccharoides</i> .....	0.1	...	1.8	0.4	1.0	0.6	0.7	1.1	...
<i>Bouteloua hirsuta</i> .....	8.5	4.0	3.6	...	...	...	1.7	T	...
<i>Paspalum plicatulum</i> .....	...	9.5	...	...	...	...	...	...	...
<i>Panicum</i> spp. (perennial).....	0.3	10.8	0.3	0.5	5.1	3.1	0.9	0.8	3.4
<i>Manisuris cylindrica</i> .....	...	0.4	0.3	3.5	4.5	1.2	...	1.7	...
Forbs.....	1.0	1.2	0.6	1.1	0.3	0.4	0.8	0.1	0.8
Total.....	31.3	54.8	77.2	75.2	74.2	80.6	75.4	75.6	57.7
Basal Density (Percent).....	1.2	2.2	7.0	3.3	2.3	4.0	3.6	4.5	1.2
<i>Species that Invade</i>									
<i>Eragrostis intermedia</i> .....	0.2	2.4	1.8	2.1	7.9	8.8	2.4	14.3	5.8
<i>Paspalum ciliatifulum</i> .....	...	1.7	0.3	3.0	2.7	2.0	1.7	7.9	8.8
<i>Buchloe dactyloides</i> .....	...	0.9	...	3.3	...	0.3	...	...	...
<i>Sporobolus neglectus</i> .....	...	0.2	...	1.3	...	0.2	...	...	1.4
<i>Chloris verticillata</i> .....	...	...	...	5.1	6.2	2.2	10.8	0.8	8.9
<i>Schedonnardus paniculatus</i> .....	...	...	...	4.0	3.0	1.1	0.7	...	0.5
Other grasses <sup>4</sup> .....	...	0.1	T	T	1.0	T	1.1	0.1	0.5
Forbs.....	...	T	0.4	1.4	2.5	3.1	5.8	0.7	13.8
Total.....	0.2	5.3	2.5	20.2	23.3	17.7	22.5	23.8	39.7
Basal Density (Percent).....	T	0.2	0.2	0.9	0.8	0.9	1.1	1.4	0.8
Total Basal Density.....	3.9	4.0	9.0	4.4	3.2	5.0	4.8	5.9	2.0

<sup>1</sup> Mowed annually, grazed from August to May during favorable years; remaining fields grazed yearlong.<sup>2</sup> Acres per animal unit month.<sup>3</sup> Other grasses each making up less than 0.3 % of the composition include *Paspalum floridanum*, *Andropogon eliottii* and *Festuca octoflora*.<sup>4</sup> Other grasses each making up less than 0.5 % of the composition include *Setaria geniculata*, *Cenchrus pycnanthus*, *Paspalum dilatatum*, *Cynodon dactylon*, *Tridens tridens*, *Andropogon virginicus*, *Hordeum vulgare*, *Agrisotis hiemalis* and *Phalaris caroliniana*.

The remaining fields studied were grazed continuously at the stocking rates listed in Table 2. It will be noted that Fields 6 through 13 are arranged according to grazing intensities, i.e., Field 6 had the lightest grazing use and Field 13 was the most heavily grazed of the group.

The results indicate that little bluestem decreased readily with grazing and that heavy continuous use caused this species to disappear, especially when the acreage allowed per animal unit was less than 0.5 A per month. Side-oats grama apparently withstood grazing more effectively than other decreaseers as it diminished very gradually with an increase in stocking rates. Big bluestem, Indian grass, Florida paspalum, Elliott bluestem (*Andropogon eliottii*), and sixweeks fescue (*Festuca octoflora*) were among the decreaseers which were not found in pastures in which less than 0.5 A was allowed per animal unit month.

Field 6 received the lightest use of the pastures grazed without deferment. Although the owner al-

lowed 1.25 A per animal unit month or 15 A per animal unit year, the amount of little bluestem was only 29.5%. Observations indicated that in August of 1950 there was considerable forage remaining for fall and winter use.

The major decreasing forbs in the order of their importance in the climax areas are:

## PERENNIALS

<i>Houstonia nigricans</i>	<i>Lepachys columbaris</i>
<i>Krameria secundiflora</i>	<i>Astragalus crassicaupus</i> Nutt.
<i>Schrankia nuttallii</i>	<i>Engelmannia pinnatifida</i>
<i>Liatris punctata</i>	<i>Scutellaria australis</i>
<i>Fimbristylis puberula</i>	<i>Silphium asperum</i>
<i>Juncus interior</i>	<i>Polygala alba</i> Nutt.
<i>Delphinium virens</i>	<i>Pentstemon cobaea</i>
<i>Psoralea floribunda</i>	<i>Salvia azurea</i>
<i>Carex festucacea</i>	<i>Cyperus globulosus</i>
<i>Oxalis stricta</i>	<i>Senecio plattensis</i> Nutt.
<i>Acacia hirta</i> Nutt.	

## ANNUALS

*Bifora americana*      *Centaurea americana*  
*Valerianella stenocarpa*      *Castilleja indivisa*  
*Rudbeckia bicolor*      *Linum rigidum*  
*Lesquerella gracilis* (Hook.) S. Wats.

Texas grama and Texas wintergrass were the important increasers in most stages of retrogression. The data in Table 2 indicate that Texas grama increased from the composition percentage of 4.8 in the climax to 61.2% on areas with a stocking rate of 0.61 A per animal unit month. The amount of this grass diminished in fields utilized at heavier rates.

Texas wintergrass increased more slowly than Texas grama with increasing stocking rates and attained approximately 33% of the composition in the most heavily grazed pastures. The two annual three-awn grasses, prairie three-awn (*Aristida oligantha*) and Kearney three-awn (*A. intermedia*), although relatively unimportant in the composition, increased gradually and reached their highest percentage in the most heavily grazed pasture. Tall dropseed, hairy grama (*Bouteloua hirsuta*), Carolina jointtail (*Manisuris cylindrica*) and brownseed paspalum (*Paspalum plicatulum*) responded in a manner similar to Texas grama. Each of these species increased and then decreased with an increase in stocking rate. Silver beardgrass, Heller panicum (*Panicum helleri*) and roundseed panicum (*P. sphaerocarpon*) were erratic in composition changes with increasing intensities of utilization.

The principal forbs that increased with grazing are in order of importance:

## PERENNIALS

*Ruellia nudiflora*      *Tragia nepetaefolia*  
*Neptunea lutea*      *Aster ericoides*  
*Aster phyllolapis*      *Petalostemon candidus*  
*Dichondra repens*      *Callirrhoe involucreta*  
*Monarda punctata*      *Cirsium discolor*  
*Phyllanthus avicularia*

## ANNUALS

*Plantago rhodosperma*      *Gnaphalium falcatum*

Plains lovegrass (*Eragrostis intermedia*) was an early and important invading species in the prairie. Fringeleaf paspalum (*Paspalum ciliatifolium*), buffalo grass (*Buchloe dactyloides*) and puffsheat dropseed (*Sporobolus neglectus*) appeared early also. Other grasses including knotroot bristlegrass (*Setaria geniculata*), mat sandbur (*Cenchrus pauciflorus*), dallisgrass (*Paspalum dilatatum*), Bermudagrass (*Cynodon dactylon*), longspike tridens (*Tridens strictus*), broomsedge bluestem, little barley (*Hordeum pusillum*), winter bentgrass (*Agrostis hiemalis*) and Carolina canarygrass (*Phalaris caroliniana*) were never more than 0.5% each of the composition and were found only in pastures where less than 1.25 A were allowed per animal unit month. Tumble windmillgrass (*Chloris verticillata*) and tumblegrass (*Schedonnardus paniculatus*) were the most im-

portant grasses which invaded under conditions of heaviest utilization.

The major forbs which invaded were primarily annuals. In order of their importance the forbs are as follows:

## PERENNIALS

*Ambrosia psilostachya*      *Sesbania drummondii*  
*Phyla incisa*      *Asclepiodora decumbens*  
*Verbena halei*

## ANNUALS

*Gutierrezia dracunculoides*      *Croton monanthogynus*  
*Gutierrezia texana*      *Iva ciliata*  
*Gerardia fasciculata*      *Helenium tenuifolium*  
*Croton lindheimeri*      *Euphorbia bicolor*  
*Diodia teres*      *Erigeron canadensis*

In terms of percentage composition the forbs were relatively unimportant in all fields except 13. The total amount of forbs was 16.1% of the composition in this field and consisted primarily of *Gutierrezia* spp. and *Gerardia fasciculata*. The forbs in the other fields seldom exceeded 4.0% of the composition.

The total basal density of all vegetation was greatest in Field 7 where it was 9.0%. The basal densities were lower under the lightest and heaviest stocking rates than in moderately grazed pastures.

Trends in composition of the decreasers, increasers, and invaders as related to the degree of utilization showed marked differences in the lightly grazed pastures as compared with ungrazed pastures. The relative proportion of the increasers and invaders remained nearly equal through a rather wide range of heavy use; however, these two classes approached each other in importance in the field which was most heavily grazed.

Figure 3 adapted from Tables 1 and 2, shows the percentage composition of three of the principal species, little bluestem, Texas grama and Texas wintergrass plotted against stocking rates.

The important point to be drawn from the foregoing discussion is that little bluestem cannot withstand heavy grazing, especially when it is grazed without deferment. Although Field 5 was grazed only when regrowth occurred after mowing, it apparently was grazed too heavily during the nine months' season.

Texas grama increased rapidly with an increase in stocking rate, yet it eventually succumbed to overgrazing. Texas wintergrass on the other hand, seemed to be favored by continued heavy use. Figure 4, a view representative of Field 7, shows a pasture in which Texas grama had reached its highest coverage and was the most important species. Heavier use no doubt would produce a cover similar to that shown in Figure 5 which is representative of Field 13, the most heavily grazed pasture found in the area. Under the heaviest stocking rate, the majority of the plants consisted of annual species of *Gutierrezia* and spotted beebalm (*Monarda punctata*).

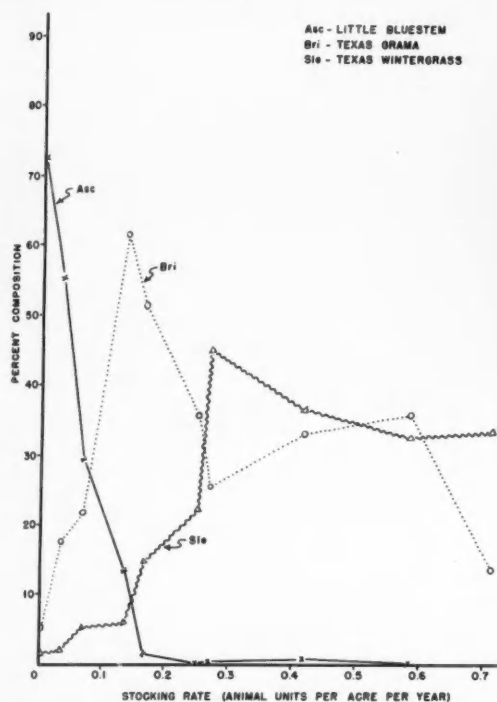


FIG. 3. The responses of little bluestem, Texas grama and Texas wintergrass to progressively heavier utilization by livestock.



FIG. 4. A typical view of Field 7 stocked yearlong at the rate of 0.61 A per animal unit month. The major species is Texas grama which comprises more than 60% of the vegetation.

#### INCREASE IN DENSITY OF MESQUITE

Mesquite was found on about 24% of the San Antonio Prairie (Figure 1). Nearly 70% of the southern part of the prairie contained trees in stands of various densities. The coverage decreased progressively in a northerly direction until less than 1% of the upper end of the prairie was covered with mesquite trees.

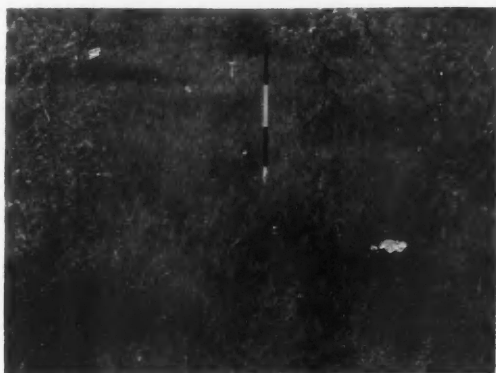


FIG. 5. Pasture 13 in which only 0.12 A per animal unit month was allowed in a yearlong grazing practice. Annual species of *Gutierrezia* are the most conspicuous plants forming a nearly uniform stand. Note the small mesquite trees on both sides of the photograph.

It was pointed out earlier that the area of greatest mesquite concentration in Texas is located to the west and southwest of the San Antonio Prairie, which probably accounts for the greater density in the southwestern end of the prairie. The progressive decrease of trees northeastward would indicate invasion from a southern source.

Mesquite was growing in four of the grazed pastures selected for intensive study (See Table 2 for grazing treatment and composition of the herbaceous vegetation). Field 8 was characteristic of areas with relatively light stands. The trees were scattered fairly evenly throughout the pasture and ranged from 0.25 to 12 in. in diameter at the base of the trunk. Crowns varied between 1 and 13 ft. in diameter.

The crown coverage was greatest in Field 10 where it shaded 14.2% of the ground, yet the stump coverage was only 15.8 sq. ft. per A. Field 13 had a crown density of 7.0% while the stump coverage was 22.6 sq. ft. per A, greater than recorded for Field 10. Field 11 had a comparatively low mesquite crown coverage of 5.0%, and a corresponding stump area of 10.0 sq. ft. per A.

The majority of mesquite plants in all fields were seedlings and immature trees and were less than 3 ft. tall, with stems averaging less than 1/2 in. in diameter. These were interspersed among the scattered mature trees, indicating that mesquite is increasing rapidly in areas where it has become established.

The shading effect of the mesquite canopies developed in this area was not sufficient to prevent grasses from growing beneath the trees. Plants of Texas wintergrass appeared to be more abundant beneath mesquite than in the openings between the trees. This was true in situations where the branches were high enough to allow access to grazing animals as well as under trees whose low branches formed a barrier to domestic grazing animals. This relationship may be a result of the shade tolerance of this grass or a response to favorable moisture relations in the vicinity of the trees. The fields which contained



TABLE 3. Plant composition and basal density of the important species in two hay meadows which have been grazed during favorable years after removal of the hay crop.

Treatment.....	MOWED ANNUALLY GRAZED PERIODICALLY	
	14*	15†
Field Number.....		
<i>Species that Decrease</i>	Composition (Percent)	
<i>Andropogon scoparius</i> .....	69.2	67.1
<i>Bouteloua curtipendula</i> .....	3.2	1.4
<i>Andropogon gerardi</i> .....	3.1	0.3
<i>Andropogon ellipticus</i> .....	1.3	1.7
<i>Sorghastrum nutans</i> .....	0.3	5.6
<i>Paspalum floridanum</i> .....	0.1	1.1
<i>Andropogon ternarius</i> .....	...	2.5
Forbs.....	4.3	2.2
Total.....	81.5	81.9
Basal Density (Percent).....	3.3	3.6
<i>Species that Increase</i>		
<i>Aristida</i> spp. (annual).....	5.1	0.2
<i>Panicum</i> spp. (perennial).....	3.8	2.0
<i>Stipa leucotricha</i> .....	3.2	0.6
<i>Sporobolus asper</i> .....	2.5	0.9
<i>Bouteloua rigidisetata</i> .....	2.4	0.1
<i>Bouteloua hirsuta</i> .....	0.7	...
<i>Andropogon saccharoides</i> .....	0.1	...
<i>Paspalum plicatulum</i> .....	...	9.5
<i>Manisuris cylindrica</i> .....	...	2.9
Forbs.....	0.1	0.1
Total.....	17.9	16.3
Basal Density (Percent).....	0.7	0.8
<i>Species that Invade</i>		
<i>Paspalum ciliatifolium</i> .....	0.3	1.7
<i>Phalaris caroliniana</i> .....	0.1	...
<i>Cenchrus pauciflorus</i> .....	0.1	...
<i>Eragrostis intermedia</i> .....	T	...
Forbs.....	0.1	0.1
Total.....	0.6	1.8
Basal Density (Percent).....	T	0.1
Total Basal Density.....	4.0	4.5

\*Grazed from August to April, allowing 2.1 A per animal unit month. Grazed only when sufficient regrowth is present.

†Grazed from August to November during favorable years, allowing 1.2 A per animal unit month.

mesquite trees had the highest percentages of Texas wintergrass.

#### EFFECTS OF MODERATE GRAZING ON HAY MEADOWS

Evidence indicates that the hay meadows may be grazed moderately after mowing without significant alteration of the vegetational composition. The data presented in Table 3 were obtained from two hay meadows which were grazed after cutting when the regrowth was sufficient to warrant such a practice. Field 14 was grazed from August to April at the rate of 2.1 A per animal unit month, while Field 15 was grazed only from August to November at a rate of 1.2 A per animal unit month. The composition of little bluestem was nearly 70.0% in the two meadows. The percentages of the other decreaseers and increaseers compare favorably with those listed for ungrazed hay meadows in Table I. A small percentage of invaders was recorded in the two grazed meadows.

Although the amount of decreaseers was less and the percentage of increaseers was greater than in corresponding ungrazed relicts the differences were not significant.

The major distinguishing character separating the grazed hay meadows from ungrazed ones seems to be differences in hay yields. Observations indicated that grazing caused obvious reductions in hay yields. This should receive further study over an extensive period of time.

#### VEGETATIONAL RETROGRESSION IN RELATION TO MICROTOPOGRAPHY

During the course of this investigation it was noted that the majority of fields selected for intensive study exhibited an undulating surface relief in the form of "hog wallows" on the nearly level uplands and a series of microridges and microvalleys on the gentle slopes. The "hog wallows" have the appearance of small to large depressions varying in depth from 1-1½ ft. and separated by slightly raised areas (Figure 6). The B horizon is exposed on the raised areas, while the A horizon is still intact in the depressions. The depressions range from 10 to 30 ft. in width. Howard (1939) described a similar microrelief and offered as a possible explanation of its formation the self-mulching of the soils brought about by alternate wetting and drying (causing swelling and shrinking). The "hog wallow" type of topography is of minor importance because of the extensive use of much of the level upland for cultivated crops.

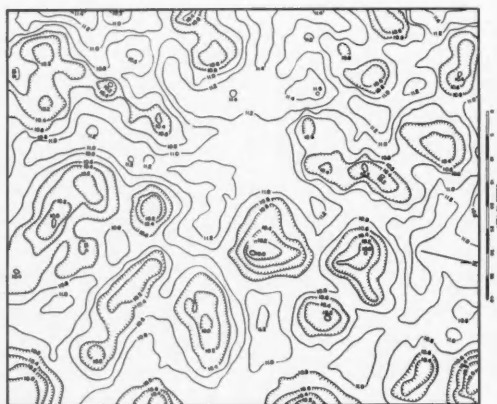


FIG. 6. Topographic map showing microrelief of "hog wallows." The contour interval is 0.2 ft.

The undulating topography of the gently sloping hillsides is more common since much of the sloping land has been reserved for hay fields and native pastures. The microridges and microvalleys alternate with each other, and run parallel with the direction of drainage. Figure 7 illustrates the undulating nature of the microtopography on a hillside studied in detail. The difference in elevation found on this area was approximately one foot from crest to trough,

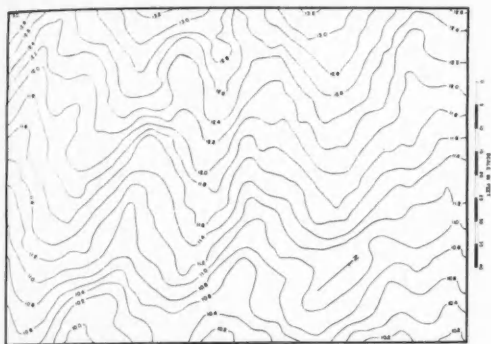


FIG. 7. Topographic map representative of microridges and microvalleys on gentle slopes. The slope is approximately three degrees and the contour interval is 0.2 ft.

and as on the upland, the B horizon is exposed on the microridges and forms a sharp contrast with the A horizon present in the microvalleys. The distance from crest to crest averages about 20 ft.

Vegetation on the microridges differed consistently from that in the microvalleys. As shown in Figure 8 the decreaseers were more important in the microvalleys than on the microridges, and there was a proportional decrease within the two sites with in-

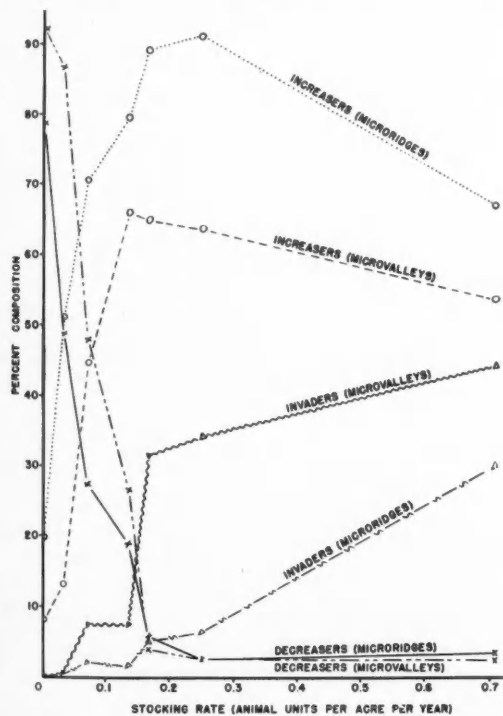


FIG. 8. Comparison of changes in plant composition of total decreaseers, increaseers and invaders from an ungrazed condition to heavy utilization on microridges and in microvalleys.

crease in grazing rates. In contrast the total increaseers made up a higher percentage of the composition on the microridges than in the microvalleys under all degrees of grazing. The invaders were of greater importance in the microvalleys throughout all areas observed.

Figure 9 illustrates how little bluestem, Texas grama and Texas wintergrass responded to grazing in the two sites. Little bluestem maintained a higher coverage in the microvalleys until it decreased to less than 15% of the composition, then it appeared to be of equal importance on both sites. The crests of the microridges constituted the most suitable habitat for Texas grama. In the ungrazed areas this species composed 12.4% of the vegetation in contrast to 0.5% in the microvalleys. Grazing animals seemed to concentrate heavily on little bluestem and other decreaseers, which allowed Texas grama to increase. This grass had the greatest increase on the microridges (Figure 9) and apparently extended its cover into the microvalleys at the expense of the decreaseers. Under light stocking rates Texas wintergrass, the other important increaseer, tended to increase in the microvalleys. Heavier stocking rate brought about a spread of this grass to the microridges. Continued heavy grazing caused the differences between vegetation occurring on microridges and in microvalleys to become less apparent.

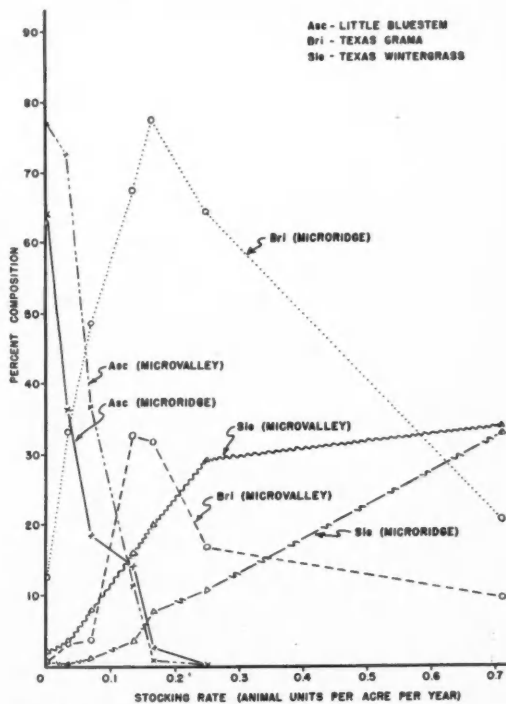


FIG. 9. Differences in the composition of little bluestem, Texas grama and Texas wintergrass on microridges and in microvalleys in the climax areas and in pastures utilized at progressively heavier rates of stocking.

The total basal density of all vegetation was nearly equal in the microvalleys and on the microridges in climax vegetation, but under most grazing intensities the density was greater on microridges. This was a result of the great increase of Texas grama on the microridges which formed a tighter cover on the surface of the soil because of its sod forming characteristics.

The microridges and microvalleys not only had different compositions of grasses but certain forbs occurred more frequently on one site than on the other. The forbs found on microridges in greater numbers than in microvalleys are:

## PERENNIALS

<i>Houstonia nigricans</i>	<i>Polygala alba</i> Nutt.
<i>Krameria secundiflora</i>	<i>Pentstemon cobaea</i>
<i>Liatris punctata</i>	<i>Neptunea lutea</i>
<i>Astragalus crassicaulis</i> Nutt.	<i>Phyllanthus avicularia</i>

## ANNUAL

*Gerardia fasciculata*

The following are forbs which occurred in greater numbers in microvalleys than on microridges:

## PERENNIALS

<i>Schrankia nuttallii</i>	<i>Engelmannia pinnatifida</i>
<i>Fimbristylis puberula</i>	<i>Aster phyllolepis</i>
<i>Juncus interior</i>	<i>Dichondra repens</i>
<i>Delphinium virescens</i>	<i>Monarda punctata</i>
<i>Oxalis stricta</i>	<i>Phyla incisa</i>

## ANNUALS

<i>Bifora americana</i>	<i>Centaurea americana</i>
<i>Valerianella stenocarpa</i>	<i>Plantago rhodosperma</i>
<i>Rudbeckia bicolor</i>	<i>Euphorbia bicolor</i>

SECONDARY SUCCESSION ON LAND RETIRED  
FROM GRAZING

Since the retrogressive changes due to grazing have been determined for this area the question arises regarding plant succession in pastures which have been released from grazing pressure. Such information is especially important in the field of range management.

The ideal situation would involve a periodic analysis of vegetation on areas subjected to progressively lighter stocking rates. Since the nature of this investigation eliminated this possibility the next best method was to find areas that had been released entirely from grazing.

Although it was impossible to determine the exact condition of the vegetation of the selected pastures at the time they were being grazed, it can be assumed from information obtained from the owners regarding past rates of stocking that the pastures were heavily grazed for a number of years prior to the removal of the livestock, consequently the average density and composition probably were similar to those presented in Table 2 for the heavily grazed pastures. Two pastures were found which had been heavily grazed and subsequently had been retired from grazing. One pasture had not been utilized by domestic

livestock for a period of 6 years and the other for a period of 20 years. The results of the line-intercept measurements are shown in Table 4. A comparison of the data in this and Table 2 indicates that under long time deferment the decrease, notably little bluestem, began to replace the vegetation favored by heavy grazing. The important increasers, Texas grama and Texas wintergrass, decreased in percentage since being retired from grazing as did most of the other increasers and invaders. The noteworthy exception to the trend was the enormous increase of silver beardgrass in the fields released from grazing. This grass never contributed more than 2.0% to the composition on the grazed pastures and hay meadows yet the areas abandoned from grazing supported an average of 30.2%. Annual *Aristida* spp. increased slightly on the pasture deferred 6 years.

Figure 10 shows the trend of little bluestem, Texas grama, Texas wintergrass and silver beardgrass from climax to an overgrazed condition under progressively

TABLE 4. Principal species and their relative importance on two areas selected to show changes which occur when pastures are retired from grazing.

Treatment	MOWED - UNGRAZED		
	6	20	
Years Retired from Grazing.			
Field Number . . . . .	22	23	Average
Species that Decrease			
Composition (Percent)			
<i>Andropogon scoparius</i> . . . . .	32.6	14.7	23.7
<i>Bouteloua curtipendula</i> . . . . .	7.4	12.0	9.7
<i>Andropogon gerardi</i> . . . . .	...	0.1	T
<i>Sporobolus asper</i> v. <i>pilosus</i> . . . . .	1.5	4.9	3.2
<i>Sorghastrum nutans</i> . . . . .	T	0.3	0.1
Forbs . . . . .	0.9	3.3	2.1
Total . . . . .	42.4	35.3	38.8
Basal Density (Percent) . . . . .	1.8	1.4	1.6
Species that Increase			
<i>Andropogon saccharoides</i> . . . . .	27.3	33.0	30.2
<i>Stipa leucotricha</i> . . . . .	10.5	15.1	12.8
<i>Bouteloua rigidiseta</i> . . . . .	6.3	7.4	6.8
<i>Aristida</i> spp. (annual) . . . . .	4.0	0.6	2.3
<i>Panicum</i> spp. (perennial) . . . . .	2.3	1.0	1.6
<i>Manisuris cylindrica</i> . . . . .	2.0	...	1.0
<i>Bouteloua hirsuta</i> . . . . .	0.4	0.7	0.5
<i>Sporobolus asper</i> . . . . .	0.2	5.3	2.7
<i>Paspalum plicatulum</i> . . . . .	T	...	T
Forbs . . . . .	0.5	1.5	1.0
Total . . . . .	53.5	64.6	58.9
Basal Density (Percent) . . . . .	2.2	2.6	2.4
Species that Invade			
<i>Eragrostis intermedia</i> . . . . .	2.7	T	1.4
<i>Paspalum ciliatofolium</i> . . . . .	0.3	...	0.15
<i>Buchloe dactyloides</i> . . . . .	0.3	...	0.15
<i>Chloris verticillata</i> . . . . .	T	...	T
<i>Phalaris caroliniana</i> . . . . .	0.1	...	0.05
<i>Sporobolus neglectus</i> . . . . .	T	...	T
<i>Andropogon virginicus</i> . . . . .	0.6	...	0.3
Forbs . . . . .	0.1	0.2	0.15
Total . . . . .	4.1	0.2	2.1
Basal Density (Percent) . . . . .	0.2	T	0.1
Total Basal Density . . . . .	4.2	4.0	4.1

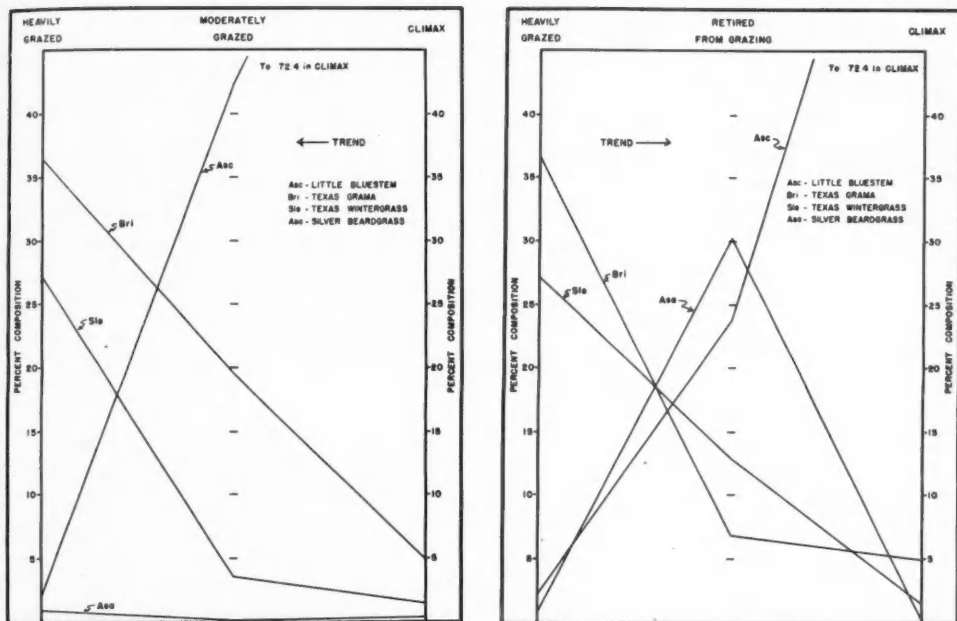


FIG. 10. The trend of little bluestem, Texas grama, Texas wintergrass and silver beardgrass in plant retrogression due to grazing compared with their trend in plant succession when grazing pressure has been eliminated.

heavier grazing and the trend from overgrazing back to climax with grazing pressure removed.

The fields which had been retired from grazing showed obvious trends of secondary plant succession. The bunches of little bluestem, for instance, ranged between 4 and 8 in. in diameter. Most of the bunches of little bluestem in the relict areas conformed to this size range, whereas the same species in pastures grazed continuously formed bunches less than 2 in. in diameter. The climax grasses as a whole appeared to be more vigorous in the abandoned pastures than in grazed ones; also, numerous seedlings were found growing among the mature grasses.

#### SECONDARY SUCCESSION ON ABANDONED CULTIVATED LAND

Although the San Antonio Prairie is an area where intensive agriculture is practiced, many sites have reverted to native grassland from time to time depending upon the fluctuations in demand for crops suitable to the area. Very few cultivated fields have been completely abandoned. A majority of them are grazed periodically. This periodic grazing generally occurs when the landowners need the additional pasture space for livestock or when grass production is sufficient to warrant grazing.

Very few fields have been abandoned for long periods of time. No doubt the value of this land for crop production discourages the owner from abandoning fields permanently. During the course of this investigation several fields which had been out of cultivation for periods of 5 or 6 years were cultivated

again when a demand for increased cotton acreage occurred in 1951.

Six fields were selected for intensive study of plant succession on abandoned cultivated land. These fields were chosen not only to represent areas abandoned for different periods of time, but because they had received the least disturbances from grazing since retirement. According to information obtained from the owners each field had been grazed only periodically or not at all. Two fields had been out of cultivation for one year, the remainder had not been cultivated for periods of 5, 6, 14 and 20 years. The results are tabulated in Table 5. Forbs averaged 49% of the composition of the vegetation of fields abandoned for one year. Horseweed fleabane (*Erigeron canadensis*) was the most important forb in Field 16, and because of its height it completely obscured the other forbs which included mat spurge (*Euphorbia supina*), white morningglory (*Ipomoea lacunosa*), slim aster (*Aster exilis*), western ragweed (*Ambrosia psilostachya*) and cudweed (*Gnaphalium falcatum*) (Figure 11). In contrast to Field 16, the important forbs in Field 17 were composed primarily of Texas snake-weed (*Gutierrezia texana*) and Tarragon snakeweed (*G. dracunculoides*). Other important species included redseed plantain (*Plantago rhodosperma*), beach gerardia, western ragweed, bitterweed (*Helenium tenuifolium*), rough buttonweed (*Diodia teres*), *Croton* spp. and spotted beebalm (Figure 12).

Texas panicum (*Panicum texanum*), an annual grass, contributed 36.2% to the composition of Field

TABLE 5. Composition and basal density of vegetation in fields retired from cultivation for various periods of time. The data representing climax vegetation have been added for convenience of comparison.

Treatment.....	GRAZED PERIODICALLY						Mowed Ungrazed
Years out of Cultivation..	1	1	5	6	14	20	Climax
Field Number.....	16	17	18	19	20	21	Hay Meadows
<i>Climax Perennial Grasses</i>							
	Composition (Percent)						
<i>Andropogon scoparius</i> .....			0.2	0.2		44.0	72.4
<i>Bouteloua curtipendula</i> .....					0.2	2.5	7.0
<i>Bouteloua rigidiseta</i> .....						4.7	4.8
<i>Scirgistrum nutans</i> .....					T	0.1	2.6
<i>Bouteloua hirsuta</i> .....						0.3	1.4
<i>Sporobolus asper</i> .....					2.7	6.3	1.8
<i>Andropogon gerardi</i> .....					0.1		1.3
<i>Stipa leucotricha</i> .....					2.3	0.5	1.2
<i>Sporobolus asper</i> v. <i>pilosus</i> .....						1.8	1.0
<i>Andropogon Elliottii</i> .....					0.1		0.2
<i>Paspalum floridanum</i> .....							0.2
<i>Manisuris cylindrica</i> .....							0.2
Total.....			0.2	0.2	5.4	60.2	94.1
Basal Density (Percent).....			T	T	0.2	2.0	4.4
<i>Subclimax Perennial Grasses</i>							
<i>Andropogon saccharoides</i> .....			15.4	15.5	64.4	31.0	0.1
<i>Panicum</i> spp.....	1.6		0.1	8.4	6.7		0.5
<i>Paspalum plicatulum</i> .....					5.8		0.5
<i>Eragrostis intermedia</i> .....	1.6	1.7	5.3	3.0	2.4		
<i>Andropogon virginicus</i> .....				4.2	3.8		
<i>Paspalum ciliatifolium</i> .....		2.2	0.2	0.5			
<i>Schedonnardus paniculatus</i> .....			0.9	0.1	0.3		
<i>Setaria geniculata</i> .....				0.7			
Total.....	1.6	3.3	23.9	32.1	83.9	31.0	1.1
Basal Density (Percent).....	T	T	0.5	0.5	2.2	1.0	0.1
<i>Other Perennial Grasses</i>							
<i>Paspalum dilatatum</i> .....			23.2				
<i>Sorghum halepense</i> .....		2.1	0.3			0.1	
Total.....		2.1	23.5			0.1	
Basal Density (Percent).....		T	0.5			T	
<i>Annual Grasses</i>							
<i>Aristida</i> spp.....	28.0	45.7	54.5	7.1	3.5		1.2
<i>Sporobolus neglectus</i> .....	17.5		1.6				
<i>Phalaris caroliniana</i> .....	0.3	0.1	0.1	T			
<i>Cenchrus pauciflorus</i> .....			0.3				
<i>Festuca octoflora</i> .....					0.1		0.1
<i>Panicum texanum</i> .....	36.2						
<i>Leptochloa filiformis</i> .....	7.0						
<i>Digitaria sanguinalis</i> .....	6.0						
Total.....	49.2	45.8	46.1	56.2	7.2	3.5	1.3
Basal Density (Percent).....	0.1	0.3	1.0	0.9	0.2	0.1	0.1
Forbs.....	49.2	48.8	6.3	11.5	3.5	5.2	3.5
Basal Density (Percent).....	0.1	0.3	0.1	0.2	0.1	0.2	0.2
Total Basal Density.....	0.2	0.6	2.1	1.7	2.7	3.3	4.8

16, but was not found in Field 17 where prairie three-awn, Kearney three-awn and puff-sheath dropseed made up 45.5% of the vegetation. Climax perennial grasses were not found in either field; however, an average of 2.5% of the composition was made up of subclimax perennial grasses.

The composition of the vegetation in fields abandoned for periods of 5 and 6 years was very

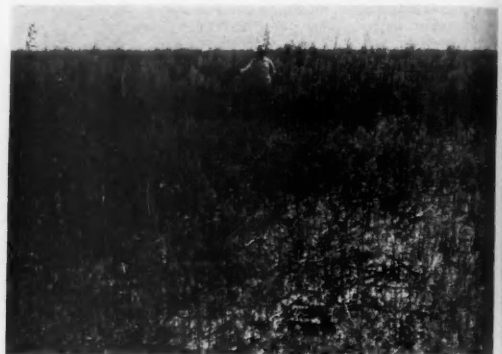


FIG. 11. Field 16 after being retired from cultivation for one year. Horseweed fleabane is the major forb and dominates the general aspect.



FIG. 12. Field 17 abandoned from cultivation for one year. Annual species of *Gutierrezia* and western ragweed are the important forbs. A comparison with FIG. 11 indicates the great diversity of plants that may invade a newly abandoned cultivated field.

similar in many respects. It will be noted in the tabular data that the annual species of *Aristida* comprised 45.7% of the vegetation in Field 18 and 54.5% in the other. Silver beardgrass which did not occur in fields abandoned for one year had almost the same percentage in 5- and 6-year-old fields. The only outstanding difference between Fields 18 and 19 was the presence of dallisgrass in Field 18, while none was recorded in Field 19.

The most noteworthy differences between fields abandoned for periods of 5 and 6 years and those abandoned for one year were the increase of *Aristida* spp., the invasion of silver beardgrass and the decrease of forbs in the fields which had been abandoned for the longest period of time. Figure 13 illustrates the appearance of a 6-year-old field dominated by *Aristida* spp. and with scattered bunches of silver beardgrass.

Field 20 had been retired from cultivation for 14 years at the time it was sampled. Several climax perennial grasses, including side-oats grama, Indian grass, big bluestem, tall dropseed, Texas wintergrass and Elliott bluestem grew in this field. These climax grasses contributed only 5.4% to the total composi-





FIG. 13. Vegetation in Field 19 allowed to develop six years after abandonment from cultivation. Most of the plants consist of annual species of *Aristida* and forbs. The taller scattered plants are bunches of silver beardgrass.

tion. Although little bluestem does not appear in the tabular data, several widely scattered bunches of this species were present in the 14-year-old field.

Silver beardgrass was by far the most important plant in Field 20. Sublimax perennial grasses constituted a total of 83.9% of the composition and it comprised 64.4% of this amount (Figure 14). Among the annual grasses, *Aristida* spp. made up 7.1% of the composition. Forbs were relatively unimportant, contributing only 3.5%.



FIG. 14. Field 20 which had been abandoned from cultivation for 14 years. Silver beardgrass is the most important species present.

The principal forbs present in fields abandoned from one to 14 years are as follows:

#### PERENNIALS

<i>Monarda punctata</i>	<i>Ruellia nudiflora</i>
<i>Ambrosia psilostachya</i>	<i>Physalis mollis</i>
<i>Oxalis stricta</i>	<i>Juncus interior</i>
<i>Dichondra repens</i>	<i>Fimbristylis puberula</i>
<i>Aster ericoides</i>	

#### ANNUALS

<i>Diodia teres</i>	<i>Gnaphalium falcatum</i>
<i>Helenium tenuifolium</i>	<i>Chrysopsis pilosa</i>
<i>Gutierrezia</i> spp.	<i>Gerardia fasciculata</i>
<i>Croton</i> spp.	

After 20 years of abandonment 60.2% of the vegetation consisted of climax perennial grasses. Little bluestem was definitely the most important of this group. Silver beardgrass was the only sublimax perennial grass present. Annual species of *Aristida* and forbs occurred only in small amounts. It is significant that perennial forbs characteristic of climax vegetation made their appearance at this period of time following abandonment from cultivation. These included bluet (*Houstonia nigricans*), trailing krameria (*Krameria secundiflora*), yellow neptunia (*Neptunia lutea*), sensitivebrier (*Schrankia nuttallii*) and dotted gayfeather (*Liatris punctata*).

Assuming that plant succession on abandoned cultivated land will eventually result in climax vegetation, the climax hay meadow data have been added to Table V for the purpose of comparison.

From simultaneous analysis of vegetation on fields taken out of cultivation for various periods of time, three distinct stages of plant succession can be recognized from the data presented. They are as follows: (1) forb and annual grass stage; (2) sublimax perennial grass stage; and (3) climax perennial grass stage.

Figure 15 illustrates the trend from early abandonment to climax of the major grasses and the forbs. There is a close similarity of change in composition of silver beardgrass in plant succession on abandoned cultivated land and on abandoned grazed land (compare Figures 10 and 15). The data indicate that

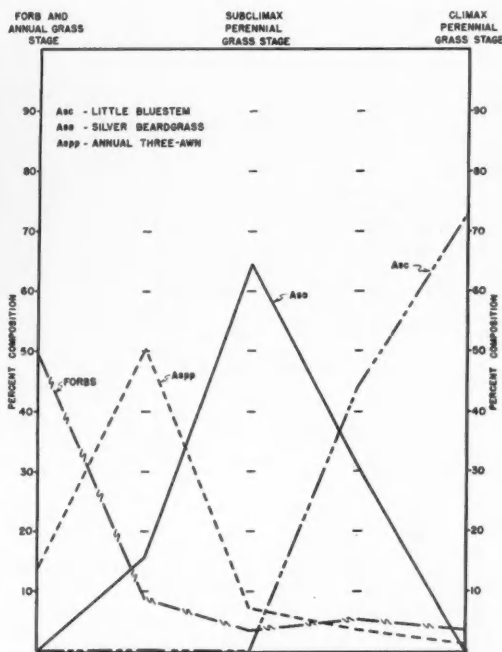


FIG. 15. Changes in composition of little bluestem, silver beardgrass, annual species of *Aristida* and forbs in the different stages of plant succession on abandoned cultivated land.

this species played an important role in each sere, especially in the intermediate stages of secondary succession. This was the most outstanding characteristic common to both. Although plant succession in the two seres may be expected to culminate in the same climax vegetation, only the late stages leading to this probably would have much in common. Plant succession on abandoned cultivated land begins from a completely denuded area in which certain soil characteristics have been altered greatly by mechanical disturbances, whereas there are remnants of perennial vegetation already established on abandoned grazed pastures. The soils of the latter also do not undergo the changes associated with cultural practices. Considering the differences associated with the two seres it becomes readily apparent that silver beardgrass reaches its greatest importance only in areas which are recovering from some sort of disturbance.

#### SEASONAL DEVELOPMENT OF THE VEGETATION

Data relative to seasonal development of the plants were collected by making regular weekly trips during 1950 and 1951 over a selected one-mile course in the San Antonio Prairie. The route included vegetation representative of reliets, grazed pastures and abandoned cultivated lands. The important species of plants were recorded on each trip and their phenological stages noted. Plants in the vegetative stages were collected whenever necessary for later identification when individuals with flowering parts became available.

Each community had many species of plants growing together and completing their life cycles at various times during the year. However, only a relatively small proportion of the species was conspicuous and formed the different seasonal aspects due to differences in abundance, height and attractive flowers.

#### EARLY SPRING ASPECT

In general the early spring appearance of the hay meadows was that of the dormant erect vegetation, composed of the previous year's growth of grasses. Some of the leaves were matted down, yet most of the culms of little bluestem, Indian grass and side-oats grama were still standing and completely obscured the basal growth and small seedlings. This drab brown color persisted unbroken from March 10, which was the average date of the last spring frost until March 25. During this time groundplum milk-vetch (*Astragalus crassicaupus* Nutt.) and spring-beauty (*Claytonia siliensis*) were in full bloom, but because of their short stature they were hidden by the old growth of grasses.

The early spring appearance of grazed pastures and abandoned cultivated fields was much the same as the hay meadows; however, the pastures were dominated by dead plants of *Gutierrezia* spp. The abandoned fields showed a gray color due to the old stems of silver beardgrass and annual three-awn grasses.

#### SPRING ASPECT

In 1951, March 25 marked the beginning of flower-

ing of many spring plants. Numerous clumps of prairie scurfpea (*Psoralea floribunda*) dotted the hay meadows and because of their height were a conspicuous part of the relief vegetation during the entire spring. Many plants flowered during March, April and May; nevertheless the general aspect of the ungrazed reliets was not changed perceptibly until early April when definite societies of common gold-stargrass (*Hypoxis hirsuta*) became conspicuous. Also, societies of eveningprimrose (*Oenothera speciosa*) bordering the depressions of the uplands added much color to the general view. Next in importance was the white color of numerous racemes of white polygala (*Polygala alba* Nutt.) which were slightly taller than the surrounding plants. The large plants of prairie scurfpea stood out well above the small grasses and old growth; however, the flowers were not easily seen. By late April the hay meadows had a definite green color. The old stalks and leaves, although still standing, became hidden by the new vegetation. The most striking sight at this time was that of scattered plants of cobaea pentstemon (*Pentstemon cobaea*) which occurred mainly on the uplands.

During the first part of May the relief areas had a bright green color which formed a background for several widely scattered plants of Engelmann daisy (*Engelmannia pinnatifida*) and Indian plantain (*Cacalia tuberosa*). During the latter part of May and early June the aspect shifted from a general view of green to one of nearly pure white with the profuse flowering of prairie-bishop (*Bifora americana*). This was the most conspicuous aspect of the spring season, since the flowers were slightly taller than the grasses and of sufficient numbers to completely overcome the green color of the understory. Late spring societies of pinewoods coneflower (*Rudbeckia bicolor*) in the microvalleys of the hay meadows added yellow to the dominating white throughout.

The heavily grazed pastures did not exhibit the colorful spring societies characteristic of the ungrazed areas. The color gradually shifted from dark brown to green as the grasses increased in height, although this was preceded by the new growth of *Gutierrezia* spp. in the microvalleys during April and May which formed a sharp contrast with the dark brown microridges.

The old growth in the abandoned cultivated fields dominated the general appearance during most of the spring; however, new growth of the annual three-awn grasses and silver beardgrass changed the color to green. The green cast was rapidly replaced in the older abandoned fields by one of white when silver beardgrass produced flowerstalks.

#### SUMMER ASPECT

By June 15, most of the spring flowers of the hay meadows were mature except prairie scurfpea which continued to bloom and stood out in unmowed meadows until the last part of July. Small societies of purple basketflower (*Centaurea americana*) and scattered yellow flowers of *Silphium* spp. were also conspicuous in the hay meadows during June and

early July. Although mowing interrupted the developmental stages of climax vegetation, observations made at the time of cutting indicated that perennial grasses dominated the general view.

Large socrs of *Gutierrezia* spp. gave the grazed pastures a bright green color in mid-summer and by August 1 their yellow flowers began to appear and blend with the dominant green of the background. Taller plants of snow-on-the-mountain (*Euphorbia bicolor*) appeared during the last two weeks of August. The white bracts of these plants were conspicuous in all of the pastures.

The fields which had been abandoned for one year either had a late summer aspect of horseweed fleabane or one of *Gutierrezia* spp. Fields abandoned 5 or 6 years supported numerous plants of *Croton* spp. and western ragweed which stood out above the shorter plants of the annual three-awn grasses during late summer. The oldest abandoned fields still presented the general white appearance of silver beardgrass which continued to flower during the summer period.

#### FALL ASPECT

The hay meadows produced considerable regrowth during the late summer of 1950. The societies of dotted gayfeather and of heath aster (*Aster ericoides*) were conspicuous during most of the fall. Scattered plants of leafybract aster (*Aster phyllolepis*) and azure sage (*Salvia azurea*) which were taller than the other plants formed a contrast with the green understory of grasses. Many of the climax grasses flowered during the fall and obscured most of the shorter forbs.

By November 25, all but a few of the plants were past the flowering stages and the vegetation began to develop a brown color, especially during the fall of 1951 when the first frost occurred late in October.

The grazed pastures and abandoned fields had the same appearance that prevailed during late summer, except the lightest grazed pastures contained many conspicuous plants of slim aster. The plants of *Gutierrezia* spp. had produced many more flowers than were present during late summer; thus yellow was the dominant color of many grazed pastures and a few abandoned fields.

#### WINTER ASPECT

The general appearance of all fields during the winter season changed from light brown to dark brown as the vegetation became dormant and the top growth began to die. This condition remained practically unchanged from early December until late March.

The fall drought of 1950 apparently caused the vegetation to remain dormant during the ensuing winter. Drought conditions also prevailed during the spring and summer months of 1951; consequently, the vegetation was dwarfed considerably and was forced into dormancy as early as July in many parts of the prairie.

#### SUMMARY AND CONCLUSIONS

The San Antonio Prairie was mapped from a vegetational survey and studies were conducted during 1950 and 1951 to determine the following: (1) the course of plant retrogression from climax on grazed native pastures; (2) trends of secondary plant succession on pastures retired from grazing; and (3) stages of secondary plant succession on abandoned cultivated land. Fields representing different stages of plant succession and retrogression were selected for vegetation analysis. Line-interception and belt transect measurements were made to determine percentage composition and basal density of the vegetation in each field.

1. A map showing the boundaries of the San Antonio Prairie is presented. The prairie is in the form of a long belt situated in southeast-central Texas.

2. Cemeteries and hay meadows which were used exclusively for hay production were found to be the most representative reliets of climax vegetation. The meadows used in this investigation had never been cultivated and had not been grazed by domestic livestock for over 50 years. Line-interception measurements indicated that little bluestem averaged 72.4% of the climax vegetation. Species of secondary importance in the climax included Texas grama, side-oats grama, big bluestem, hairy tall dropseed and Indian grass. Silver beardgrass and Texas wintergrass were among the species of minor importance in the climax areas. The total basal density of the vegetation was 4.8%.

The data presented indicate that the San Antonio Prairie is an *Andropogon scoparius* consociation and is a part of the True Prairie described by Weaver & Clements (1938).

3. The plants of the prairie may be grouped according to their responses to grazing. Under utilization by livestock the species react in the following manner; certain species decrease in importance with grazing; some species increase in percentage under utilization by livestock; and certain plants invade grazed pastures and are not found in ungrazed areas. Little bluestem was the important decreaser and was found only in small amounts in pastures which had a stocking rate of 0.5 A or less per animal unit month. Other decreasers included side-oats grama, big bluestem, hairy tall dropseed and Indian grass. The majority of the decreasing forbs were perennials.

Texas grama and Texas wintergrass were the important increasers. The former increased rapidly with grazing but diminished under heavy utilization. The latter increased steadily under moderate utilization and continued to maintain a high percentage in the most heavily grazed pastures. Texas grama and Texas wintergrass comprised a combined total of more than 60% of the vegetation in the grazing disclimax. Increasers of secondary importance included prairie three-awn, Kearney three-awn, tall dropseed,

silver beardgrass, hairy grama, Heller panicum and roundseed panicum. The principal forbs in this category were mainly perennials.

Plains lovegrass, fringeleaf paspalum, puffsheath dropseed and buffalo grass constituted the important grasses which invaded under moderate grazing conditions. Tumble windmillgrass and tumblegrass were important in pastures which were heavily grazed. The majority of invading forbs were annuals.

4. Mesquite occurs on 24% of the San Antonio Prairie. The greatest concentration is located in the southwest end, and the amount decreases toward the northwest extension of the Prairie.

5. The data obtained from sampling two grazed hay meadows indicated that periodic moderate grazing will maintain a vegetation composition similar to that found in ungrazed native meadows. However, the hay yields of grazed meadows were considerably lower than on similar ungrazed areas.

6. Microtopographical features in the form of "hog wallows" on the level uplands and alternating micro-ridges and microvalleys on the gentle slopes were evident in most of the fields. The vegetation showed consistent differences associated with microrelief. The decreasers consisting mainly of little bluestem were most important in the microvalleys under no grazing and moderate utilization. Heavy utilization by livestock caused little bluestem to be replaced in the microvalleys by Texas wintergrass and invading species. Texas grama increased mainly on the micro-ridges. In the most heavily grazed pastures Texas grama had spread to the microvalleys and Texas wintergrass had moved onto the microridges resulting in a nearly uniform cover of the two species.

7. Removal of grazing animals from heavily utilized pastures resulted in definite trends of secondary plant succession. Little bluestem, big bluestem and Indian grass increased gradually toward the climax stage. Texas wintergrass and Texas grama decreased in percentage when grazing pressure was removed. Silver beardgrass had a marked temporary increase following the removal of livestock. Side-oats grama, hairy tall dropseed and the annual three-awn grasses showed responses similar to silver beardgrass except the increase was relatively small. The invading species tended to disappear under long time deferment from grazing.

8. Plant succession on areas abandoned from cultivation may be divided into the three following stages: (1) forb and annual grass stage, dominated by annual forbs and grasses; (2) subclimax perennial grass stage, dominated by silver beardgrass; and (3) climax perennial grass stage with little bluestem as the major dominant. Although there was considerable variation in plant populations the first year, the annual three-awns were the important grasses. Fourteen years following abandonment silver beardgrass played the important role in the subclimax perennial stage. Within 20 years after retirement from cultivation most of the climax perennial grasses had appeared and substantially increased. Little bluestem showed the greatest increase in this group and such

a trend indicated clearly that the vegetation was developing toward the climax stage represented by the ungrazed hay meadows. The basal density of the major species increased steadily with time. On fields abandoned for 20 years the basal density approached that of climax vegetation. Fields abandoned for the longest periods of time supported forbs characteristic of the relict areas.

9. Silver beardgrass played an important role in plant succession on abandoned cultivated land and this same trend was indicated in plant succession on areas released from grazing. Texas wintergrass was the most conspicuous species in the grazing disclimax and constituted one of the most important plants throughout the San Antonio Prairie because of its association with heavy grazing. The vegetational classifications presented previously indicated that several authors considered silver beardgrass and Texas wintergrass to be the important climax dominants of this and similar prairies in Texas. It was pointed out in the review of the history of the San Antonio Prairie that this area has been used more or less consistently since early settlement for both grazing and other agricultural practices. This has created many areas of vegetational disturbance. Since Texas wintergrass is most apparent on overgrazed land and silver beardgrass constitutes the major species on sites recovering from soil or plant disturbances, the relicts in which little bluestem plays the important role may have been so obscured that they were overlooked by the early investigators. The data presented in this investigation indicate that under conditions of least disturbance little bluestem is the major dominant of the climax vegetation and silver beardgrass and Texas wintergrass are of minor importance.

10. The climax vegetation was characterized by successive waves of flowering subdominants which formed the seasonal aspects. Early spring societies of groundplum milkvetch and springbeauty were practically hidden by the previous year's growth of grasses. Societies of prairie scurfpea, common goldstargrass, eveningprimrose, white polygala and cobaea pentstemon in March and April, and large societies of prairie-bishop and pinewoods coneflower during May comprised the spring aspect of the ungrazed areas. Basketflower centaurea and *Silphium* spp. were conspicuous in the hay meadows during the summer season, while societies of dotted gayfeather and *Aster* spp. were numerous during the fall.

Areas representative of the grazing disclimax did not have the colorful spring flowers of the ungrazed vegetation. The summer and fall aspects of *Gutierrezia* spp. and snow-on-the-mountain euphorbia were most outstanding on grazed areas.

The appearance of abandoned crop land was dominated mainly by grasses, especially fields which had been abandoned for more than 6 years. Societies of horseweed fleabane, *Gutierrezia* spp. and western ragweed were conspicuous during the summer and fall seasons in recently abandoned fields.



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# HABITS AND ADAPTATIONS OF THE GREAT PLAINS SKINK (*EUMECES OBSOLETUS*)

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## TABLE OF CONTENTS

	PAGE		PAGE
INTRODUCTION .....	59	BREEDING .....	69
METHODS AND MATERIALS .....	60	GROWTH .....	71
DESCRIPTION .....	61	FOOD HABITS .....	74
RELATIONSHIPS .....	61	PREDATION .....	78
HABITAT .....	62	PARASITISM .....	79
BEHAVIOR .....	65	NUMBERS .....	80
MOVEMENTS .....	67	SUMMARY .....	81
		LITERATURE CITED .....	82

## INTRODUCTION

The present field study was made chiefly on the University of Kansas Natural History Reservation in Douglas County, northeastern Kansas, six miles north northeast of the University of Kansas campus. The Reservation was described and its history briefly set forth by Fitch (1952). The Reservation lies within a broad ecotonal zone where many kinds of animals typical of the eastern deciduous forests reach their western limits and other kinds typical of the interior grasslands reach their eastern limits.

Since 1948 the Reservation has been protected and maintained as a natural area. Earlier, the more open parts of it were grazed. On these former pastures the establishment and spread of forest species is proceeding rapidly, and successional changes have resulted in habitat improvement for many kinds of animals. For other kinds, including the Great Plains skink, the steady deterioration of habitat has reduced the numbers of individuals and the area occupied. The skink's preferred habitat is in open situations, with rocks and low thick grass and herbaceous vegetation for shelter.

According to the best available evidence, at the time the area was settled, a prairie type of vegetation predominated, maintained by the effect of fire and the heavy grazing of large native mammals. As a result of these influences deciduous forests were localized and chiefly confined to such protected situations as river flood plains and north slopes. With the advent of agriculture and the control of prairie fires, the forest trees and shrubs and their community associates spread to the upland situations that were not under cultivation. On areas that

were heavily grazed, advance of the woodland either was held in check completely or it was much slowed, with selection of types most resistant to browsing or most tolerant of it.

The Great Plains skink (*Eumeces obsoletus*) is one of the larger kinds of lizards in the United States. Although it has an extensive geographic range in the southwestern states and northern Mexico, no thorough study of its habits and ecology has heretofore been made. More or less casual observations made at different times and places, by several workers have been recorded in the literature.

The species was originally described (as *Plestiodon obsoletum*) by Baird & Girard (1852), from "Valley of the Rio San Pedro of the Rio Grande del Norte". In this same issue of the Proceedings of the Philadelphia Academy of Sciences Hallowell (1852) described as *Lamprosaurus guttulatus* a young individual of the same species. The distinctive coloration and pattern of the young long misled later workers into recognizing both as distinct species, until Burt (1929) finally relegated *guttulatus* to the synonymy of *obsoletus*.

Professor E. Raymond Hall has critically examined the manuscript and has made many helpful suggestions. Mr. Richard B. Loomis aided me with the field work by tending live-traps at various times. Also he made available to me many live skinks collected at various localities in eastern Kansas, and he identified chiggers found on the skinks, and provided information concerning them. Mr. Dennis G. Rainey and Mr. Richard Freiburg contributed several live skinks. Dr. Robert L. Gering contributed a specimen found hibernating, and through the

kindness of Mr. Dwight Platt and Mr. Benjamin Zerger, I was able to include the observations that Mr. Zerger made on this skink at the time it was found. Mrs. Louise Brunk made the drawings and graphs for Figs. 3, 5, 6, 7 and 11.

#### METHODS AND MATERIALS

Most of the Great Plains skinks studied were captured either by hand where found under sheltering rocks, or in live-traps. In April and early May, especially after heavy rains, the skinks have been sufficiently activated by warm weather to emerge from their hibernation sites, although they still are not fully active, and tend to stay in hiding, in burrows beneath flat rocks that are warmed by direct sunlight. At such times they can be found and caught in numbers. At other times, this method of collecting was seldom successful, as the skinks were much harder to find in their hiding places, and when uncovered, they usually rushed away and escaped into sheltering vegetation, or into holes and crevices.

Live-trapping was a far more effective method of obtaining the skinks. Cylindrical wire traps with funnel entrances at each end (Fitch 1951) were carefully placed along the bases of rock outcrops, and were covered with flat rocks for shelter from sunshine. Many of the traps used were provided with valvelike transparent doors at the funnel openings, to prevent exit of the trapped animals. These doors were essential for trapping some kinds of snakes and lizards, which soon would have escaped from traps lacking them. For Great Plains skinks, however, traps from which the doors were missing were nearly as effective. In keeping with their predilection for burrowing, the trapped skinks tended to keep on the bottoms of the traps in their efforts to escape, and therefore usually failed to find the funnel openings. Most of the traps used were approximately one foot long and five inches in diameter. Of the 634 captures recorded on the Reservation 458 were made in these funnel traps. A few juveniles were caught in pitfalls, which were also effective for catching the smaller kinds of lizards, and toads, but were not deep enough to prevent adult Great Plains skinks from escaping.

Each skink taken on the Reservation was marked by toe-clipping (Fitch 1952) and was released again at the point of capture. Items of information ordinarily recorded at each capture included: means of capture, toe formula identifying the individual, sex, snout-vent length, tail-length (with original and regenerated parts recorded separately), weight, location, ectoparasite infestations, injuries or deformities, and occasionally the body temperature. Snout-vent length was obtained by holding the skink against a rigid transparent millimeter ruler and exerting a gentle pull on each end until the animal was straightened to its full length but not abnormally stretched. Ordinarily this could be accomplished only by waiting for several minutes until fatigue caused the skink to relax. The powerful body mus-

culture rendered this skink difficult to measure accurately. To attain reasonably consistent readings it was essential to attain approximately the same degree of relaxation, and this required patience and experience. A live skink's body is so elastic that the reading may vary over a range of many millimeters, depending on the relative amounts of tension exerted by the skink itself and by the person handling it. In skinks that are cold and partly torpid the muscles seem to be in a state of tonic contraction, and stretching to full length is less easily accomplished than in those that are warm and fully active. Measurements were recorded to the nearest millimeter. In 66 instances, individuals were found to have been recorded as slightly shorter than at an earlier capture. Most of these apparent reductions in length involved discrepancies of only 1 mm or 2 mm. The margin of error was normally less than 2%, rarely up to 5%. Substantial gains of 10 mm or more in snout-vent length were easily detectable within the limitations of the method used, and were ordinarily accompanied by corroborative increase in tail-length and weight. Tails, being less flexible and muscular than the bodies, were more easily measured, but it was necessary to use extreme care, because a skink might snap off its tail with a sudden flip while it was being handled. This occurred on a few occasions. Weight to the nearest gram was obtained by tying the skink in a small cloth bag and suspending it from the hook of a Chatillon spring scale. The margin of error was approximately 1 gm unless air movement interfered. Juveniles, for which the margin of error by this method constituted a relatively high percentage, were often brought to the laboratory and weighed on a balance to an accuracy of .1 gm.

Sex was determined by holding the skink with its ventral surface upward, and pressing lightly upon the ventral side of the tail at its base. The anal opening was thereby caused to gape, and one or both of the hemipenes sometimes everted. At least the edge of the hemipenis was exposed in the male. This technique was effective only for adults and subadults. Sex was not known for most individuals smaller than 100 mm in snout-vent length, until they were recaptured after attainment of maturity.

Data used in this report were obtained over a five-year period (1949-1953). It seems best to present the findings at this stage as the steady decline in the numbers of skinks over the period of the study has greatly reduced the opportunities for obtaining further data. By September 30, 1953, a total of 634 captures had been recorded for 208 individuals. Of the 208 total, 93 were caught just once; 132 were each taken in only one of the five consecutive years of the study, while 76 had records in more than one year.

During the same period, a similar field study of the common five-lined skink (*Eumeces fasciatus*) was made on the same general area. For this smaller and more numerous species more complete data were obtained, permitting a better understanding of its ecology, and these data have been used as the basis

for a separate report. In the present report, the findings concerning the five-lined skink are occasionally utilized for comparison and contrast with the Great Plains skink. *Eumeces fasciatus* is more typical of the genus and more primitive in many respects than is *E. obsoletus*.

### DESCRIPTION

Taylor (1936) listed the characters of the genus and described the osteology of *Eumeces obsoletus*, and he characterized it as: "A large species, lacking typical, medial, dorsolateral and lateral white lines; young black with white spots on upper and lower labials, and on other head scales except loreals and temporals; pitting on scales dim in young but still evident in adults; outer preanal scales overlapping inner; subcaudals widened; postgenials large, bordered by a scale longer than wide; one or no postnasal; two postmentals (rarely one); nuchals small; lateral scale rows usually diagonal; usually 26 or 28 scale rows about the middle of the body." The dorsal coloration varies from grayish brown or yellowish brown to olive, with irregular black markings (Fig. 1). Each black marking is mainly confined to a single scale. In specimens from Kansas the black is concentrated in the dorsolateral and lateral areas, and tends to form a broad lateral stripe and a narrow dorsolateral stripe on each side. In southern populations the pattern is somewhat different, with less black pigment and the black is on the edge of each scale of the dorsal and lateral surface, not concentrated into stripes, and there is little or no black on the tail.



FIG. 1. Adult female Great Plains skink showing bodily proportions and color pattern,  $\frac{1}{2}$  natural size.

Distinctive characters of the Great Plains skink, including proportions of the limbs, head, and body, seem to be correlated with its incipient fossorial adaptation. Because of its burrowing habits, it has been able to invade regions that are more arid than those occupied by most of the North American members of the genus. Because of large size, individuals may be less subject to desiccation than are those of the smaller species of *Eumeces*. The torso tends to be cylindrical with the dorsoventral diameter almost as much as the lateral diameter, whereas in most other species, the body is somewhat depressed. The torso is relatively thicker than in other species. The neck is especially thick and muscular, of a diam-

eter approximately equal to that of the body and wider than the head. The limbs and tail are relatively short and stubby. The hind foot (measured from heel to tip of claw on fourth toe) ranged from 13.4% to 18.1% in a series of eight specimens of various sizes, while in a comparable series of *E. fasciatus* it ranged from 18.5% to 21.4%. The toes of both front- and hind-feet usually have somewhat fewer dorsal scales and ventral lamellae than have the longer toes of *E. fasciatus*. The claws of *E. obsoletus* are proportionally longer than those of *fasciatus*, and noticeably less curved. Curvature of the claws in *fasciatus* evidently is correlated with its tree-climbing habits. On the soles of the forefeet in *E. obsoletus* there are many small granular scales and several enlarged scales of pyramidal shape (Fig. 2).

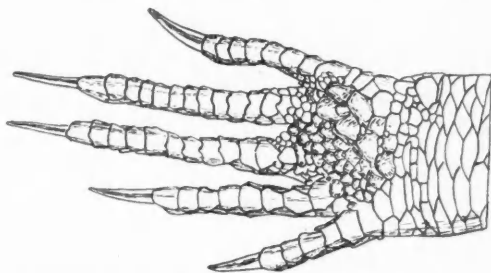


FIG. 2. Palmar view of left forefoot, showing powerful claws, and pyramidal palmar scales that render it effective for digging, 6 times natural size.

These modified scales evidently aid in digging by providing a rasping surface to loosen or remove particles of soil. In *E. fasciatus* the corresponding scales, being flattened, are not especially adapted for digging. In *E. obsoletus* sexual dimorphism is almost lacking, and the sexes are distinguished with difficulty even in the breeding season. In large adult males of *E. obsoletus* the heads are a little more swollen in the temporal regions than are heads of females. On the contrary, in *E. fasciatus* and most other species of the genus there is pronounced sexual dimorphism in proportions of head, body and limbs, and especially in the male's early loss of the juvenal pattern, with red suffusing the head region in the breeding season.

### RELATIONSHIPS

The genus *Eumeces*, to which the Great Plains skink belongs, is widely distributed within the warmer parts of the northern hemisphere, both in the New World and in the Old World (Taylor 1936). The Great Plains skink represents one of 15 natural groups within the genus. Its nearest relatives, the only other members of its group, are three Oriental species, *E. kishinouyei*, *E. corensis*, and *E. chinensis* (with subspecies *chinensis* and *pulcher*). As compared with these species, *E. obsoletus* seems to have progressed farther in its divergent evolution, having completely lost the original striped pattern characteristic of most forms of *Eumeces* and having the

scale rows on the sides oblique rather than parallel. *E. kishinouyei* of the Riu Kiu Islands differs in its much larger size and seven-lined pattern with mid-dorsal line extending anteriorly onto the head and bifurcating, limbs relatively long, dorsal and lateral scales striated in adults. *E. chinensis* has a five-lined pattern (not extending anteriorly onto the head) and it lacks a postnasal. In color pattern and some other characters these Oriental skinks seem to be transitional between *E. obsoletus* and the five-lined skinks of the *fasciatus* group.

Pope (1929) wrote concerning the habitat of *E. chinensis*: "I have observed this to be the common skink of plain and plateau. It abounds along roads, paths, irrigation terraces, and similar places all through the open flat country and low 'grass mountains.'" Concerning *E. elegans*, a near relative of the North American five-lined skink which occurs in the same part of the Orient as does *E. chinensis*, Pope stated: "This species is obviously a mountain form never seen on the open irrigated plain of the plateaus and valleys." Thus it seems that the divergence in habitat preferences observable in *E. obsoletus* and *E. fasciatus* where they occur in the same region in Kansas and Oklahoma also applies, in a general way at least, to their Oriental representatives, *E. chinensis* and *E. elegans*, respectively. Within the genus, the *obsoletus* group and the *fasciatus* group probably had already diverged both structurally and ecologically at a time in the early Tertiary when North America and Asia had a land connection with a moderate climate permitting them to disperse into both continents. The land connection must have either included sufficiently diverse habitats to accommodate both types simultaneously, or else must have undergone change in its climate and vegetation, permitting first one group and then the other to make the intercontinental migration.

In its geographic range *Eumeces obsoletus* overlaps eleven other species of the genus, namely *E. fasciatus*, *E. laticeps* and *E. anthracinus* near its eastern limits, *E. septentrionalis* throughout much of the eastern part of its range, *E. brevilineatus* and *E. tetragrammus* in the southeast, and *E. multivirgatus* in a large area in the northwestern part of its range, and in the southwest, *E. gilberti*, *E. gagei*, *E. callicephalus* and *E. taylori* (Fig. 3).

#### HABITAT

Occurring over a wide and diverse geographic range, from the mixed woodland and prairies of western Missouri and eastern Oklahoma to the Arizona deserts, this skink is obviously adaptable to a great range of habitat conditions. The most widely used vernacular name, "Sonoran skink", seems inappropriate, as the only authentic record from the Mexican state of Sonora known to me is the recent one by Cliff (1953), and the distribution does not correspond well with the Sonoran life-zones. The

name, Great Plains skink, used in the latest checklist (Schmidt 1953), is much more descriptive. The geographic range is roughly co-extensive with approximately the southern half of the Great Plains, the southern part of the North American Grassland Biome. Where the species occurs in regions that are chiefly forest or desert, it is limited to small areas that differ from those surrounding them in having short thick grass or other ground vegetation, and in having flat rocks for shelter.

Maslin (1947) wrote that on the plains of eastern Colorado these skinks are found in dense low vegetation, near rock outcroppings, or beneath trash and rocks. Moore & Rigney (1942) observed that in Payne County, Oklahoma, the species frequently occurs about old buildings.

In the southwestern part of its range the species seems to be increasingly confined to rugged terrain. Authors specifically mentioning habitat have in most instances found this skink on mountain slopes or in canyons. Evidently the Great Plains skink is rare or absent in the intervening stretches of desert plains. Blair (1950) recorded it from the Oklahoma panhandle in broken mesa- and canyon-habitat. Strecker (1915) wrote that it is common in the canyons and breaks of the Texas panhandle, and in the southern plains and trans-Pecos counties of the state. Bailey (1905) listed *E. obsoletus* as characteristic of the Upper Sonoran Life-zone. He mentioned occurrence at the south end of the Guadalupe Mountains at 6800 ft. "... well toward the upper edge of the Upper Sonoran Zone", and at other localities of several thousand feet elevation. Smith & Buechner (1947) listed *Eumeces obsoletus* as one of the many reptiles occurring on the Edwards Plateau (a dry limestone area of scrub oak woodlands) in western Texas, which are limited on the east by the Balcones Escarpment. Mosauer (1932) wrote that in the Guadalupe Mountains it seemed to be common although it was inconspicuous because of its secretive habits. He noted that it utilized as hiding places crevices in rocks or spaces under logs, or beneath loose bark, or in bushes, and especially the spaces between the leaves of dry sotol. Milstead, Mecham & McClintock (1950) recorded the Great Plains skink in the mesquite-creosote association of the Stockton Plateau.

Little (1940) wrote that in the Roosevelt Reservoir area of central Arizona these skinks were found in leaf litter on the ground in chaparral-woodland of the Upper Sonoran Life-zone, but were uncommon. Gloyd (1937) mentioned finding specimens beneath stones at 5400 ft. in Carr Canyon, Huachuca Mountains, and others in a stone pile on the sloping plain 2½ mi. southeast of the Huachuca Mountains. Quaintance (1935) recorded one found under a stone at the top of Rose Peak, 8787 ft. in Greenlee County, Arizona.

In Kansas the many locality records are clustered



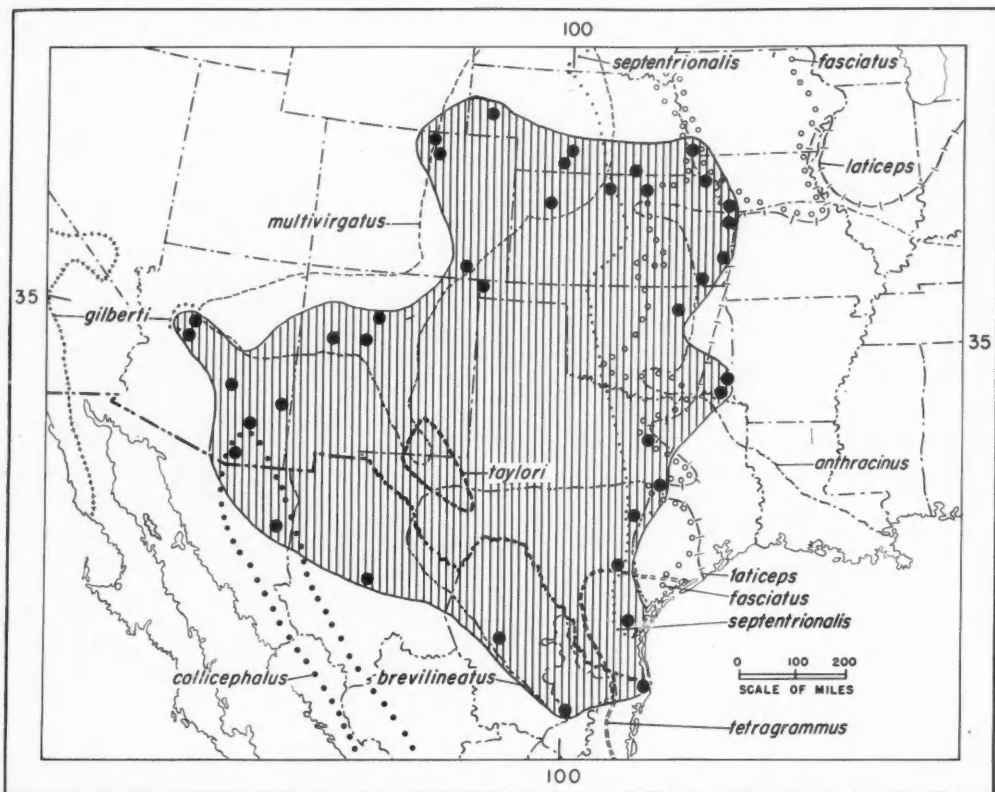


FIG. 3. Map of the range of *Eumeces obsoletus* (shaded), with dots showing marginal records, in Iowa (Bailey, 1943), Nebraska (Hudson, 1942; R. B. Loomis, MS), Missouri (Anderson, 1942), Kansas (Smith, 1950), Colorado (Taylor, 1936), Oklahoma (Taylor, 1936; Blair, 1950; Trowbridge, 1934), New Mexico (Taylor, 1936), Arizona (Taylor, 1936; Little, 1940; Gloyd, 1937), and Mexico (Smith and Taylor, 1950; Cliff, 1953).

Range limits of other species of *Eumeces* that overlap the range of *E. obsoletus* are shown. For the species *anthracinus*, *fasciatus*, *laticeps* and *septentrionalis*, the known limits of the range to the west are shown; for *brevilineatus*, *callicephalus*, and *tetragrammus* the known limits to the north are shown; for *gilberti* the known limits of the range to east are shown; for *taylori* the entire range is outlined; and for *multivirgatus* the entire range except the northern end is shown. One other species, *E. gaigei*, occurs in parts of New Mexico and adjoining states, mainly within the range of *obsoletus*. Note that a large area in the central part of the range of *obsoletus* is not shared with other species, as it lies between the ranges of one group mainly eastern in distribution, and another group mainly western, but that almost all marginal areas of the range are shared with competing species.

mainly in the eastern and north-central parts with few in the southern parts and hardly any in the northwestern quarter. There is some correspondence with major grassland types as mapped by Gates (1937). The records fall almost entirely within areas indicated as bluestem and bluegrass, and hardly any are within an area designated as typical shortgrass (buffalo and grama grasses) which occupies more than one-third of the state in its western part.

Taylor (1936) stated that the Great Plains skink is found most frequently on open hillsides where there are rock exposures or scattered flat rocks, but that in the absence of rocks the species burrows in the open and is much more difficult to find. He noted it to be rare, or at least difficult to find and collect, except in eastern Kansas. "Here it is not difficult

to obtain, for I have collected two or three dozen individuals of this species in one day. . . ."

My own observations agree with those of Taylor, but the best day's catch has amounted to only 18 skinks of this species. While few herpetologists can expect to equal Professor Taylor's prowess as a collector, habitat deterioration probably has occurred in the 20 years or more that have elapsed since the time of the field observations he recorded. Persistent raids by commercial collectors have reduced the numbers of these large slow-breeding lizards, locally at least.

The species probably reaches its maximum abundance in the Flint Hills region, a north-south belt extending across Kansas approximately three-fourths of the distance from the western to the eastern

border, with extensive limestone outcrops and low rolling hills, dominated by such grasses as grama, big bluestem and little bluestem. The entire area is used primarily as cattle range. Controlled burning in early spring is an almost universal practice by landowners. As a result there is but little ground litter, and vegetation is scanty, especially during the spring. The vegetation type and conditions in general that are created by the combination of burning and heavy grazing, favor the Great Plains skink. Its partly subterranean habits evidently permit it to escape destruction in grass fires, and ordinarily it is still in hibernation when they occur. A new crop of grass and other low vegetation has begun to grow by the time of its emergence.

In situations where conditions are xeric and where vegetation is extremely sparse because of severe burning or overgrazing, these skinks are likely to be absent or scarce. I have found them in greatest numbers in areas that are protected from the recurring prairie fires, as along outcrops adjacent to moist gully bottoms supporting some shrubby vegetation, or on steep and extremely rocky slopes of ravines where burning is incomplete and patches or tussocks of vegetation are left intact. In the Flint Hills, *Eumeces obsoletus* was the only kind of reptile I found at some localities but at other localities it was in association with one or more of the following: *Diadophis punctatus*, *Tropidoclonion lineatum*, *Coluber constrictor*, *Lampropeltis dolia*, *Tantilla gracilis* and *Crotaphytus collaris*. At localities where habitat conditions seemed to be optimum in the Flint Hills, I have often found that most of the movable flat boulders had been turned or shifted; under these conditions usually but few skinks were found, and on occasion none at all. This intensive collecting has been mainly in areas adjacent to well travelled public roads and doubtless there are many less accessible stations of occurrence where the habitat remains undisturbed and the population remains in its original abundance.

Burt (1928b) described various habitats occupied by the species in different parts of Kansas, including thickly wooded hillsides (Douglas County), isolated sandstone outcroppings in a treeless area (Washington County), limestone ledges in dips of valleys, but not on the hilltops (Butler County). In a later publication Burt (1933) wrote that this kind of skink is typically an inhabitant of the prairie-ledge formations, but he mentioned one individual that lived in a hole at the base of a large tree and others that ran to small holes in the ground in grassy situations where no rocks or other solid objects were in evidence. Smith (1950) stated that it is found most commonly on grassy or somewhat wooded hillsides underneath loose, flat, limestone rocks, usually in rough country, although it may be found even on flat prairie if there are enough burrows of mammals to afford protection. Gloyd (1928) wrote that it was found most often under stones on prairie hillsides or sparsely wooded pastureland.

The Flint Hills are near the eastern limit of the

range, and farther east the skink becomes increasingly scarce and localized. It barely reaches the eastern border of Kansas and the western edge of Missouri. In Douglas County where the Reservation is situated, and in neighboring Leavenworth, Jefferson, Shawnee, and Anderson Counties, I have observed Great Plains skinks in several dozen localities, but always in smaller numbers and more localized colonies than in the Flint Hills. In this more eastern area it is usually found in heavily grazed upland pastures where there are limestone outcrops or ledges (Fig. 4). Usually such pastures are dominated by coarse weeds such as hoary vervain, ironweed, and ragweed, indicative of overgrazing, but with some bluegrass or brome.



FIG. 4. A hilltop limestone outcrop in a heavily grazed pasture  $\frac{1}{4}$  mile WNW from the University of Kansas Natural History Reservation, in Jefferson County, Kansas, June 20, 1954, showing habitat typical of the Great Plains skink in the northeastern part of its range. The low vegetation is mostly ironweed (*Veronica interior*).

On the Reservation approximately a dozen individuals were found in woodland. All but two of these were at well scattered points in the relatively small part of the woodland that had been heavily browsed and grazed by livestock through 1948, and they were all in the more open parts of these woods. The two taken in ungrazed woodland were at the base of an old rock wall approximately 100 ft. from the edge of a hilltop field. A few others were caught at scattered points in a bottomland field, formerly overgrazed pasture; most of these were along the edges of a deep gully, especially where there were rocks. However, by far the greatest number of captures were in two hilltop areas totalling only a few acres. One of these was the site of an old deserted quarry, an open rocky and weedy area of approximately an acre. The other, "Rat Ledge" (Fig. 5), was approximately 750 ft. of a limestone outcrop with the adjacent edges of a hilltop field and a sparsely wooded slope. Elms and hackberries, mostly small or medium sized, grew along the ledge, and the woods below this ledge was open, with elms, hackberries, walnuts, and honey locusts, and with a sparse undergrowth of coralberry, dogwood, crabapple, and wild plum. Evidently these shrubs were held in check by grazing, whereas in adjacent parts

of the woodland protected from grazing for a decade or more before 1948, they formed thickets along the hilltop edges. Under such conditions skinks were not found. Along Rat Ledge, however, there were, in 1948, scarcely any shrubs except for large, well spaced clumps of sumac (*Rhus trilobata*). The steady encroachment of other shrubs and coarse weeds that occurred in the following five year period, had nearly eliminated the skinks by 1953, and this stretch of ledge was beginning to assume the same aspect as other hilltop edges where livestock had been fenced out for a decade or more and thickets of underbrush had grown up.

### BEHAVIOR

I have seen a total of several dozen individuals in the open, but usually only as they escaped to shelter and disappeared. They were never more than a few feet from the cover provided by rock clefts or dense vegetation, such as clumps of *Rhus trilobata*. They were quick to take advantage of such shelter and usually disappeared within a few seconds. Usually they easily eluded my attempts to capture them. In almost every instance when such individuals were seen in the open, temperatures were in the nineties or high eighties (F), and the skinks were fully active and alert.

Effect of temperature on extent of surface activity may be indicated to some extent, by the numbers caught in funnel traps in different months: April 4, May 43, June 73, July 140, August 160, September 36, October 2.

Earliest dates on which these skinks were found in different years were: April 24, 1949; April 7, 1950; April 19, 1951; April 2, 1952; April 2, 1953; April 18, 1954. Mr. Benjamin Zerger described to me (*in litt.*) his discovery of a hibernating juvenile on January 5, 1951, in Newton, Harvey County, Kansas. While digging close to the foundation of a house, in loose, moist, black loam, in which were mixed particles of wood and other construction materials, he came upon the skink curled up at a depth of approximately 18 inches. No burrow or crevice was in evidence.

In hibernation this skink tolerates temperatures a few degrees below freezing, but probably it cannot survive being frozen solid. In the autumn of 1953, several skinks were kept on an outdoor porch, in a container open on top and with a shallow layer of soil on the bottom. Only partly buried in the soil, they were able to survive night air temperatures that were frequently below freezing, and once as low as  $-5^{\circ}\text{C}$ , as recorded on a maximum-minimum thermometer a few feet away.

On April 19, 1953, near Eskridge, Wabaunsee County, Kansas, four skinks that were found under rocks when the air temperature was  $6^{\circ}$  to  $7^{\circ}\text{C}$ , did not move until they were handled, and then were slow and feeble in their movements. On the following day, observed in the laboratory at  $7^{\circ}\text{C}$ , these skinks were partly active, and were able to crawl stiffly and slowly across a table top. Collared lizards

(*Crotaphytus collaris*) found in the same habitat were completely immobilized and helpless at this same temperature. Each year Great Plains skinks were found beneath flat rocks several weeks before any were seen in the open or caught in traps. On May 11, 1952, 13 found under rocks had body temperatures ranging from  $19.0^{\circ}$  to  $30.2^{\circ}\text{C}$ , and air temperatures ranged from  $13.5^{\circ}$  to  $18.5^{\circ}\text{C}$ . Those skinks having the lowest temperatures, near  $20^{\circ}\text{C}$ , were in burrows in the damp soil, still nearly concealed when the overlying rocks were turned, and they attempted to escape by withdrawing into the holes. Those with the highest temperatures, near  $30^{\circ}\text{C}$ , were on the soil surface, in contact with overlying rocks, and they were much more active and attempted to escape by running. In 1953 the first one seen in the open was noticed on the University campus at Lawrence, basking at the edge of a sidewalk at 5 P.M. on April 20, and it darted back into a hole under the sidewalk. Air temperature was approximately  $12^{\circ}\text{C}$ , and the concrete slab of the sidewalk was only slightly warmed on its upper surface by the sunshine.

The skinks found in burrows under rocks were usually warm to the touch. Their body temperatures were mostly higher than air temperatures because of their positions in contact with the undersides of sunshine-warmed flat rocks. For 30 individuals taken beneath rocks on various dates, the skink body temperature, and the air temperature nearby in the open (shown in parentheses) were as follows (in degrees Centigrade):

April 2, 1953.  $30.5^{\circ}$  ( $21.0^{\circ}$ ),  $26.5^{\circ}$  ( $20.5^{\circ}$ ),  $19.7^{\circ}$  ( $12.3^{\circ}$ ).

May 11, 1952.  $19.0^{\circ}$  ( $13.5^{\circ}$ ),  $20.2^{\circ}$  ( $16.2^{\circ}$ ),  $20.2^{\circ}$  ( $16.2^{\circ}$ ),  $24.2^{\circ}$  ( $18.5^{\circ}$ ),  $29.5^{\circ}$  ( $16.2^{\circ}$ ),  $30.2^{\circ}$  ( $16.2^{\circ}$ ),  $20.2^{\circ}$  ( $17.2^{\circ}$ ),  $24.2^{\circ}$  ( $17.2^{\circ}$ ),  $24.2^{\circ}$  ( $17.2^{\circ}$ ),  $27.3^{\circ}$  ( $17.8^{\circ}$ ),  $29.0^{\circ}$  ( $16.2^{\circ}$ ),  $24.3^{\circ}$  ( $16.2^{\circ}$ ),  $23.8^{\circ}$  ( $18.5^{\circ}$ ); May 19, 1951.  $28.2^{\circ}$ ; May 20, 1951.  $33.3^{\circ}$ ; May 21, 1952.  $17.5^{\circ}$  ( $21.7^{\circ}$ ); May 31, 1953.  $35.0^{\circ}$  ( $29.7^{\circ}$ ),  $31.5^{\circ}$  ( $29.7^{\circ}$ ),  $35.0^{\circ}$  ( $29.7^{\circ}$ ),  $32.7^{\circ}$  ( $29.7^{\circ}$ ).

June 2, 1951.  $21.6^{\circ}$  ( $23.8^{\circ}$ ),  $21.6^{\circ}$  ( $23.8^{\circ}$ ).

July 18, 1951.  $23.8^{\circ}$  ( $24.4^{\circ}$ ),  $25.0^{\circ}$  ( $24.4^{\circ}$ ),  $25.0^{\circ}$  ( $21.6^{\circ}$ ).

August 15, 1951.  $31.5^{\circ}$  ( $26.9^{\circ}$ ); August 16, 1951.  $29.4^{\circ}$ .

On only six occasions have I succeeded in taking temperatures of individuals caught in the open under natural conditions. Records of these follow: July 6, 1952,  $36.3^{\circ}$  ( $32.0^{\circ}$ ); May 25, 1952,  $34.8^{\circ}$  ( $26.5^{\circ}$ ); August 12, 1952,  $30.6^{\circ}$  ( $28.6^{\circ}$ ); July 25, 1951,  $29.5^{\circ}$  (air temperature not recorded); September 13, 1951,  $27.7^{\circ}$  ( $22.2^{\circ}$ ); June 16, 1951,  $23.3^{\circ}$  ( $21.6^{\circ}$ ). The individual taken on June 16, 1951, was moving about in grass that was still wet with morning dew, and was slow and sluggish in its movements, evidently having just emerged.

In July, 1952, several captive Great Plains skinks were placed in an experimental terrarium that was warmed and exposed to the sunshine at one end, and cooled with ice and shaded at the other end.

Here their frequent short movements were motivated mainly by attempts to regulate their body temperatures. For a juvenile, successive temperature readings after intervals of several minutes were: 33.3°, 32.4°, and 33.8°. For two adults, readings recorded were: 34.9° and 32.7°. At the warm end of the terrarium the metal strip was recorded at 47° on its underside. In running over it the skinks showed no signs of distress, but they speeded up their movements somewhat, and did not remain on it for more than 10 to 15 seconds. Moving off the metal they would sometimes allow a tail or foot to remain in contact with it even though the metal was, to me, uncomfortably hot to touch.

Great Plains skinks, in containers with loose, damp soil were placed in sunshine and fed on August 21, 1953, when the air temperature was 29.5° C. After a few minutes of basking the skinks raised their body temperatures beyond the optimum level, and as each one of the six began to move about restlessly, or to burrow, I caught it and recorded its temperature. These temperatures, in the order they were taken, were as follows: 34.3°, 33.8°, 35.7°, 35.1°, 33.7°, 35.8°. On August 28, 1951, one basking in the sunlit part of its cage had a body temperature of 32.4° C.

It seems that for this species optimum temperature level is approximately the same as for *E. fasciatus*, determined, with much more extensive data, to be between 31° and 34° C, and probably near the latter figure. Like *E. fasciatus* the present species tends to maintain its temperature within this narrow range by warming or cooling itself as the need arises, while it is active in the open, and it ordinarily does not allow its temperature to lower more than a few degrees at most from this range. Above the optimum, the range of safety is narrow, and an increase of only a degree or two in its temperature causes the skink to make vigorous attempts to find cooler surroundings.

The Great Plains skinks that I found in the open and captured by hand provided less than one percent of the total captures. Similarly, of some 200 specimens collected by Taylor (1936) possibly less than half a dozen were taken in the open. It seems that ordinarily these skinks do not venture out of their burrows until their body temperatures have been sufficiently raised by the insulated soil about them or by the overlying flat rocks. In this respect the Great Plains skink differs from the five-lined skink which may emerge still in a semi-torpid condition on cool spring days, depending on direct sunlight for rapid warming to a level at which it can carry on normal activities.

Great Plains skinks that were startled in the open scrambled for shelter with rapid lateral undulations of the body aiding the short legs in locomotion. On several occasions when approached slowly, skinks showed uneasiness rather than alarm, and did not immediately seek hiding places. Such individuals moved slowly, sliding the body along the ground with the head slightly raised and turned at an angle to

the body to watch movements of the observer or any other signs of possible danger. By using great caution and avoiding sudden movements, I have been able to follow such individuals for as much as 50 ft. They always kept to rock clefts or similar shelter well screened by dense vegetation. An attempt to catch such a skink by seizing it almost always resulted in its instantaneous escape into an inaccessible hiding place. Once I succeeded in noosing a large adult seen moving along a fissure at the base of a rock outcrop, where it seemed to feel secure. When the noose stick was extended toward it, either the cut end or the quivering wire attached to it distracted the skink's attention from me, and it crawled rapidly toward the noose and struck at it, apparently mistaking it for prey, as the alligator lizard (*Gerrhonotus*) and various iguanids have often been noted to do.

In captivity Great Plains skinks are less nervous and excitable than five-lined skinks, and take food more readily and thrive better. The viciousness mentioned by various authors applies only to individuals that are handled and are struggling to defend themselves; the skink does not offer to bite until it has been grasped. Other small reptiles, or mammals enclosed with captives are ordinarily neither attacked nor threatened. Skinks kept in containers having a layer of loose soil or objects to hide beneath usually kept out of sight under cover, but when cages were sprinkled with water the skinks were likely to emerge and drink greedily, even though a regular supply of drinking water was available in a pan or dish. Such captive skinks excavated burrows. Several might use the same burrow system, or parts of it, simultaneously.

A skink newly introduced into a container with loose soil might within a few minutes bury and conceal itself. With snout depressed the burrowing skink forces its head forward into the soil aided by lateral flexions of its neck, the powerful muscles exerting pressure first from one side and then from the other. The squirming movements of the muscular body are supplemented by the short forelimbs performing slow machinelike digging movements to scratch away particles of soil and scrape them back to one side. The forelegs, being shorter than the head and neck combined, are used to move soil from beneath the chin on either side. The hind feet also are used, but to a lesser extent, scooping back loose earth brought within their reach by the forefeet.

Where these skinks were abundant, as at Rat Ledge, and certain other areas away from the Reservation, they were often found in their burrows when sheltering flat rocks were lifted, exposing them. At times when the soil was loose and moist in late spring and early summer, most of the suitable flat rocks, in situations supporting high populations of the skinks, had recent excavations beneath them, often unoccupied. A burrow might lead from an entrance at one side of the rock to an exit on the other side in a fairly direct course, or a burrow might wind about, with one or more lateral branches. Most of the skinks



caught by hand were those uncovered in such situations. Reactions of an exposed skink varied according to temperature and the amount of concealment provided by the burrow system. Some skinks immediately dashed for other cover; others withdrew from view into deeper parts of their burrows. Usually such individuals were easily dug out, but an occasional burrow was so deep and well protected by rocks that the skink in it was secure from capture. Frequently an exposed skink withdrew out of sight only to break through the surface crust with its snout a few inches from the point of disappearance and attempt to escape by running.

In one exceptional instance, on May 26, 1949, near Rat Ledge, an adult, exposed by turning the flat rock that was sheltering it, ran 10 ft. to a small elm tree nearby and escaped by climbing rapidly up the vertical trunk to dense foliage more than 15 ft. above the ground. At this place, no rock clefts or holes were noticed, and the skink did not hesitate in heading for the tree.

Captive skinks were seen to find their food by both sight and scent. An active spider or insect placed in the container usually stimulated the lizard to immediate pursuit. It was characteristic of the skink to pause as it overtook the prey and prepared to lunge at it, in contrast to the behavior of more active lizards of other families—racers, fence lizards, or collared lizards—which often catch their prey on the run. The pause at close range before the final lunge may serve partly for olfactory test of the prey. Food was easily recognized by olfactory test alone. A piece of meat or a freshly killed insect might soon be noticed by a skink passing nearby,

and was grasped after a preliminary touch with the tongue.

### MOVEMENTS

On the Reservation, habitat suitable for Great Plains skinks totalled only a few acres. Being largely confined to these small areas, the skinks may not have moved about so freely as they would have where continuous habitat extended over large areas. Even within their preferred habitat they tended to stay in small areas of more than 50 ft. but less than 150 ft. in greatest diameter, for periods of weeks or months, or even years. For the 118 individuals recaptured, the maximum distances between captures averaged 77.5 ft. Eleven had made no measurable movement and 27 others were not more than 10 ft. from the point of original capture. The median movement was 40 ft. Ninety-one of the total had moved 100 ft. or less, and 27 had moved more than 100 ft.; twelve of these latter had moved more than 200 ft. It is evident that vagility varies according to age and sex. Average, median and maximum movements in feet were, for adult males 89.8, 70, and 375; for adult females 55.0, 50, and 400; and for juveniles 47.0, 35 and 375.

Several types of movements are involved. The occasional shifts to new areas cannot be distinguished with any degree of assurance from the normal movements within a home range unless the records for the individuals are unusually complete. For several, shifts seem to be clearly indicated (Fig. 7). After a series of captures near the same place such a skink would show up at a new location for a second series

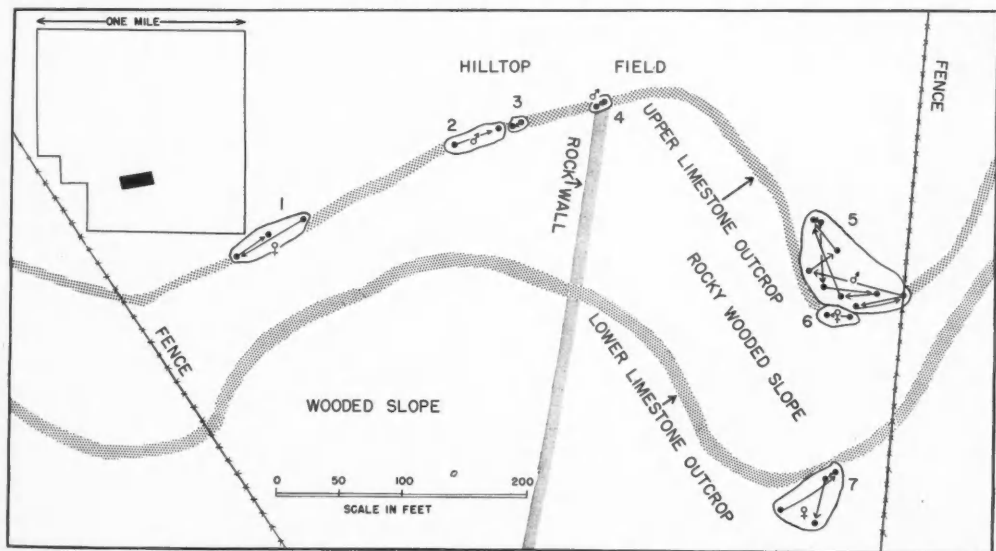


Fig. 5. Map of "Rat Ledge" study area showing chief physiographic features, and also showing successive capture points and possible home ranges of individual Great Plains skinks. Inset shows location of the study area (in black) on the University of Kansas Natural History Reservation, the section in the extreme northwest corner of Douglas County, Kansas (section 4, TWP 12S, R 20E). No. 1: Three captures in two months. No. 2: Two captures in 33 months. No. 3: Two captures in one month. No. 4: Two captures in one month. No. 5: 12 captures in 12 months. No. 6: Four captures in 11 months. No. 7: Eight captures in 22 months.



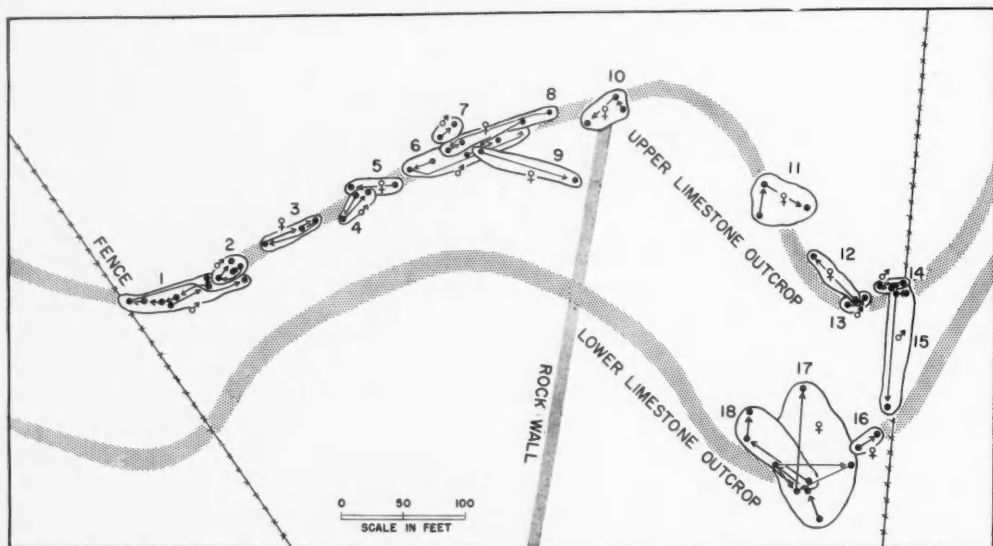


FIG. 6. Map of "Rat Ledge" study area the same as that in FIG. 5, showing successive capture points and possible home ranges of individual skinks. No. 1: Thirteen captures in 26 months. No. 2: Nine captures in 12 months. No. 3: Six captures in 24 months. No. 4: Five captures in 11 months. No. 5: Three captures in three months. No. 6: Five captures in 11 months. No. 7: Two captures in two months. No. 8: Eight captures in 4 months. No. 9: Two captures in 25 months. No. 10: Four captures in 25 months. No. 11: Three captures in 11 months. No. 12: Two captures in 11 months. No. 13: Two captures in 2 months. No. 14: Four captures in 3 months. No. 15: Three captures in 11 months. No. 16: Two captures in 2 months. No. 17: Six captures in 24 months. No. 18: Four captures in 2 months. Note that in favorable areas ranges of several or many individuals may overlap.

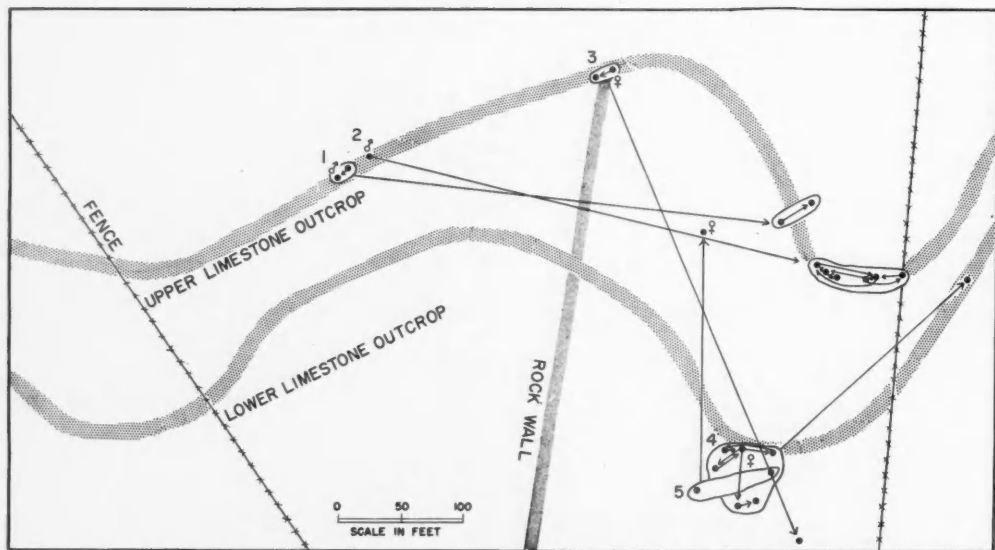


FIG. 7. Map of "Rat Ledge" study area, the same as that in FIG. 5, showing successive capture points and possible home ranges of individual skinks. These individuals made unusually long movements, evidently involving shift to new home ranges, different from those originally occupied. No. 1: Four captures in 25 months. No. 2: 18 captures in 11 months. No. 3: Three captures in 36 months. No. 4: 12 captures in 12 months. No. 5: Three captures in 14 months.

of captures clustering together. For other individuals captured only a few times, outstandingly long movements seemed to indicate that shifts had occurred. A few individuals seem to have shifted more than once. Several of these had moved back to the starting place.

Limitations inherent in the methods of catching Great Plains skinks prevented obtaining random distribution of records for individuals. Wire funnel traps could be used successfully where natural features of the terrain created likely travel routes in which skinks could be intercepted, usually along edges of rock outcrops or sunken boulders. Only one or a few such sites might be present in the area occupied by an individual skink. Most of the skinks that were caught by hand were uncovered in their burrows, but the potential sites of capture by this method were likewise usually not numerous within the small area evidently encompassed by a home range. In most of its hiding places the individual was secure from capture.

TABLE 1. Average distance in feet between points of capture. Numerals in parentheses indicate number of skinks in sample.

Age and sex classes	PROBABLY WITHIN A HOME RANGE			PROBABLY FROM AN EARLIER HOME RANGE TO A LATER ONE
	2 places	3 or 4 places	more than 4 places	shifts
Adult males....	47.5 (10)	105.6 (8)	124.6 (12)	250 (10)
Adult females....	54.2 (12)	56.0 (5)	75 (6)	290 (7)
Juveniles.....	35.5 (19)	56.6 (15)	60 (7)	255 (5)

For adults, time span of individual records was often greater than for juveniles. As a result the records for adults probably included more shifts of range. Shifts of range probably occur either by gradual encroachment a few feet at a time into new and unfamiliar areas, or by an abrupt transfer of activities from one area to another. Most of the skinks that had shifted their home ranges had undergone one or more hibernations since the original capture. Occasional shifts were recorded after much shorter intervals.

The longest movement was one of 500 ft. by a skink whose records extended over 47½ months. It was caught in 1949, 1952, and 1953. Probably this individual followed along the hilltop rock ledge instead of cutting across the intervening slopes; travel by the most direct route along the ledge would have amounted to 830 ft.

The usual concept of home range does not apply well to the Great Plains skink despite its tendency to remain within a small area. One skink may spend many days in its small burrow system under the same rock, or else if it does emerge at all it makes only short trips and then returns. But such shelters and burrow systems are temporary, generally occupied

for only a few days or, at the most, a few weeks. Then the skink moves on to another site, often only a few yards away. Later as it shifts to still other successive sites, it ordinarily does not move farther in the same direction, but tends to keep within a small area, probably using the same travel routes and depending on the same landmarks for shelter. The "home range" encompassing the area to which normal movements are confined, is, however, ill-defined, because it is covered infrequently and has no definite boundaries and its size, shape, and position are ephemeral.

## BREEDING

Sexual activity is limited to a period of weeks in late spring and the onset is delayed several weeks after emergence from hibernation. The annual breeding cycle has but slight effect on the gross appearance of the testes. In the breeding season they are slightly enlarged and turgid, approximately 10% of the skink's snout-vent length, and are nearly half as wide as long. In sexually immature males, and in mature males at times of year other than the breeding season, the testes are not only somewhat shorter, but are relatively more slender.

On May 12, 1951, at the height of the breeding season, ten males were collected in Wabaunsee County, Kansas. The seven which seemed to be sexually mature ranging from 102 to 117 mm in snout-vent length, and weighing from 19.5 to 37.6 gms, had testes 10 to 11½ mm in length and 4 to 5 mm in width. Three large young ranging from 88 to 91 mm in snout-vent length and weighing 14.7 to 16.3 gms, had testes averaging 8.2 mm in length, and 3.5 in width. In four males of 111 to 119 mm and 29.5 to 34.3 gms collected on June 3 and 7, after the breeding season, testes were somewhat smaller, 8 to 10 mm in length and 4 to 4½ mm in width. In five subadults of 95 to 104 mm collected on June 3 and June 17, testes averaged 7.6 mm long and 3.5 mm in width. No histological study of the seasonal changes in the male gonad was made. The annual cycle in all species of *Eumeces* probably follows closely the trends found by Reynolds (1943) in *E. fasciatus*.

Courtship and copulation have been described by several observers. The mating pattern followed probably is similar to that in other species of *Eumeces*. Visual recognition of the female by the male usually initiates the courtship but is invariably followed by olfactory test as the approaching male touches the female with his tongue. There is but little preliminary courtship; the male dashes in pursuit of the female, and grasps her by loose skin of the shoulder region. A minute or more afterward he loops his hindquarters beneath the female to begin copulation, which is normally of several minutes' duration.

On May 13, 1952, a male that was placed in a container with two females courted both, persistently but unsuccessfully. Neither was receptive, and one seemed to be already gravid. The male followed them about, nosing their tails and bodies. Seemingly stimulated, he would pursue, either astride a female's

hindquarters or alongside her, biting clumsily at her side, but without securing a hold. The female that seemed to be gravid, reacted violently, twitching her tail in irritation as the male approached, and opening her mouth in threat, then scrambling away to hide under any available shelter.

In late April, May and June I have often found Great Plains skinks in pairs, a male and female in the same burrow or interconnected burrows beneath flat rocks. On one occasion when such a pair was placed together in a container soon after their capture, copulation ensued within a few minutes. Probably the species is not strictly monogamous. A male having located a receptive female in her burrow system probably tends to remain there for periods of days or longer and to repulse other males that may come later, defending the burrow as a temporary small breeding territory.

On May 7, 1949, on the University of Kansas campus, a pair of large adults were found under a sunken boulder on a grassy bank. They were captured and photographed. A few minutes later when the boulder was raised again, a second smaller male was found under it, seemingly having just come there. When the female was released there, she ran and the small male followed her eagerly. The female was slow and phlegmatic in her behavior. The male overtook her approximately three feet from the point of release, and succeeded in copulating. As the pair separated, the first male was released beside the boulder. In moving about, he soon noticed the smaller male, and immediately gave chase. Both scrambled for several yards with unusually animated and brisk movements. The pursued male found concealment and escaped in a clump of bushes. After several minutes the larger male returned slowly to the vicinity where he had been captured. The female had moved several feet up the bank, and was lying on a flat rock under bushes. The male soon noticed her and approached. Several times when the female moved, he followed close behind. His behavior toward the female contrasted with the aggressive courtship of the smaller male.

Recorded dates of copulation in confinement are: April 21, April 27, and May 6 (Gloyd 1928); May 8, 1926, May 17, 1926, June 13, 1927, and June 15, 1927 (Burt 1928). On May 31, 1953, Mr. Richard B. Loomis noted copulation in a pair captured a few days earlier. On May 31, 1953, copulation was recorded in a pair collected on the same day. These ten dates indicate a spread of nearly two months in the breeding season, but in captivity abnormal matings may occur. In any one year the span of the breeding season is probably less, with variations from year to year according to weather conditions.

Of numerous females dissected, one on May 3, 1952, contained nine ovarian ova, another on May 20, 1949, contained 17 ovarian ova, and another on June 3, 1950 contained 15 ovarian ova. Two examined on June 7, 1953, contained eight and nine uterine eggs. Females laid clutches of 11, 12, and 15 eggs in captivity. Additional records of clutch size are provided

by published records: 11 (Gloyd 1928); 9 and 15 (Burt 1928); 10 (Taylor 1936); and 7 (Bailey 1943). The average for these 13 clutches is 11.4.

Laying dates recorded in the literature are: June 11-13, 1925 (Gloyd 1928); June 18, June 26, July 1, and July 1-7 (Burt 1928); July 10-14, 1941 (Bailey 1943). On July 1, 1950, a clutch of eggs was found in a terrarium where they may have been deposited a few days earlier, and other clutches have been recorded laid on June 25, 1951, June 21, 1952, and June 20-22, 1953.

TABLE 2. Length, weight, and condition of reproductive organs in adult and subadult females.

Date	Snout-vent length in mm	Weight (gms)	Sizes and numbers of ova
May 20, 1949...	120	52.2	17 (6 left, 11 right) av. 8 mm
June 3, 1950...	123	43.1	15 (6 left, 9 right) av. 9 mm
April 29, 1951...	126	38.3	30+, av. 2 mm
May 12, 1951...	115	37.5	22, av. 2 mm
May 12, 1951...	107	24.8	Numerous ova, av. approx. 1.8 mm
May 12, 1951...	118	42.3	17 (7 left, 10 right) av. 3 mm
May 2, 1951...	111	37.7	28 (12 left, 16 right) av. 2.5 mm
May 2, 1951...	100	21.0	24 (12 left, 12 right) av. 2 mm
April, 1951*	105	25.6	31 (16 left, 15 right) av. 1.2 mm
May 6, 1951...	120	43.0	25 (10 left, 15 right) av. 2.8 mm
May 6, 1951...	109	27.8	24 (12 left, 12 right) av. 1.5 mm
May 19, 1951...	108	26.1	15 (8 left, 7 right) av. 1 mm
May 19, 1951...	104	22.0	19 (9 left, 10 right) av. 1.5 mm
June 17, 1951...	113	29.9	Many ova, all less than 1 mm
June 17, 1951...	105	24.6	Many ova, all less than 1 mm
June 25, 1951...	113	36.9	Many ova, all less than 1 mm
June 3, 1951...	117	29.8	Many ova, all less than 1.5 mm
June 3, 1951...	102	20.7	Many ova, all less than 1 mm
June 3, 1951...	117	30.0	Many ova, all less than 1 mm
June 26, 1951...	104	...	Many ova, all less than 1.5 mm
May 3, 1952...	128	33.1	9 (5 left, 4 right) av. 3.2 mm
June 7, 1953...	107	30.5	8 (uterine, 4 left, 4 right) 13 x 9 mm
June 7, 1953...	116	32.6	9 (uterine, 4 left, 5 right) 13 x 8 mm

\*Late in the month.

Only five of the 23 females examined in spring and early summer, as listed in Table 2, had markedly enlarged ovarian ova, or uterine ova, indicating that they were breeding. Five, having snout-vent lengths of 105 mm or less, may have been too young to have attained sexual maturity, and four others that were taken in late April or early May may have been collected too early in the season to show well defined evidence of breeding, even though they might have produced eggs later in the season. Nevertheless, it seems that a large proportion of the adult females may fail to breed in any one season, and as a result the productivity is low. On only one occasion have I found eggs in a natural nest of *E. obsoletus*, although I have found dozens of clutches of *E. fasciatus*. Judging from the site where the *E. obsoletus* clutch was found, and the sites where gravid females were found in burrows beneath rocks, the nest burrows of *obsoletus* are much deeper and better protected than those of *fasciatus*. Perhaps one reason why so few gravid female Great Plains skinks are found is that they tend to remain in deep burrows, usually beneath massive boulders that cannot be turned. At different times, four females were kept in containers with their

clutches of eggs (Fig. 8) Each excavated a nest burrow like those seen in the field and resembling nest burrows of *E. fasciatus* except for their larger size and greater depth. Moist soil lining the nest cavity was glazed by pressure of the skink's smooth polished body as it moved about. These females rarely showed themselves above the surface of the soil in their containers. They occasionally emerged to drink when the container was heavily sprinkled with water. From time to time nests were dug up and exposed in the containers in order to observe them, and on several occasions the female with her clutch of eggs was transferred to a new container. It was characteristic of the female that she kept her clutch in a compact cluster by partly encircling the eggs with her body, and she excavated a burrow for their shelter. The nest burrow might at first be near the surface of the soil if the female had been transferred to a new container, necessitating excavation of a new burrow. But in every instance eventually the cavity was displaced downward until the eggs were resting on the bottom of the container.



FIG. 8. Adult female Great Plains skink with her clutch of eggs,  $\frac{1}{3}$  natural size.

Females differed in their reactions to disturbance when exposed in their burrows with their clutches. One would run from the nest and hide in another part of the container. Another displayed no fright but would advance toward my extended hand, examining it intently and testing it with her tongue. The females did not attempt to attack in defense of their eggs, nor did they open their mouths in threat, as brooding females of *E. fasciatus* often do under similar circumstances.

From the four clutches of eggs kept and incubated in the laboratory, only one young was hatched. Most of the eggs were attacked and destroyed by molds or fungi. Shells of several were ruptured when they were handled, despite special precautions taken in rolling them into a teaspoon, rather than by grasping them between the fingers.

On June 25, 1951, a female was found in a natural nest with her clutch, seemingly newly laid, as the shells were still clean and white. The female with her eggs was transferred to the laboratory, but eventually she deserted. The history of this clutch during their incubation is summarized in the following notes which show gradual increase in size and weight as a result of absorption of moisture. Measurements are in mm.

June 25 Sizes of six randomly selected eggs of the clutch of 12: 18.2 x 11.9; 18.2 x 11.9; 18.9 x 11.1; 18.3 x 11.3; 19.0 x 11.5; 18.2 x 11.5. Total weight of combined clutch of 12: 15.7 gms.

June 30 Lengths range from 19.1 to 18.7; widths from 12.5 to 12.0; combined weight of all 12: 15.7 gms.

July 17 Seven eggs have spoiled; sizes of remaining five: 23.8 x 14.5, 2.8 gms; 23.5 x 14.5, 2.75 gms; 22.2 x 14.2, 2.4 gms; 22.0 x 13.8, 2.3 gms; 21.3 x 13.0, 2.1 gms.

July 20 Sizes of remaining three: 24.1 x 15.0, 2.85 gms; 22.3 x 14.1, 2.4 gms; 21.1 x 13.0, 1.9 gms.

July 22 24.2 x 15.1, 2.9 gms; 22.3 x 14.0, 2.4 gms.

July 28 25.0 x 15.3, 3.2 gms; 23.2 x 14.4, 2.55 gms.

August 3 24.2 x 14.8, 3.3 gms (accidentally punctured); 23.5 x 14.7, 2.8 gms.

August 15 Remaining egg found to have hatched; snout-vent length of hatchling 35½ mm, tail 42 mm, weight 1.1 gms.

Although *E. obsoletus* produces somewhat larger clutches of eggs than does *E. fasciatus*, the reproductive potential is lower. *E. fasciatus* breeds at the end of its second year and each adult female produces an annual brood regularly thereafter, whereas in *E. obsoletus* three years or more are required to attain sexual maturity and many of the mature females seem not to participate in the annual breeding season. Lower productivity in *E. obsoletus* may be correlated with the safer existence provided by subterranean habits, and also with its larger size. Size ratio of egg to parent and of hatchling to parent is similar in both species; the hatchling averages approximately one-third of the adult's length (snout-vent), and a little less than 1/30 of the weight of an adult.

#### GROWTH

Hatching occurs in the latter half of the summer. In the southern part of the range hatching is relatively early; Mosauer (1932) stated that young were abundant at the time of his arrival on July 5 in the Guadalupe Mountains of New Mexico and Texas. In northeastern Kansas, however, hatching occurs in late July or in August or even as late as the early part of September. The recorded copulation dates indicate that the breeding season may extend over several weeks in any one year. Further spread in time of hatching may result from the shortening of incubation in clutches that are laid where they receive the maximum amount of heat from rocks or soil warmed by sunshine, and the lengthening of incubation in clutches that are in partly shaded sites where soil temperatures average lower. Earliest recorded appearance of hatchlings on the Reservation each year of the study were as follows: July 28, 1949; August 9, 1950; August 15, 1951 (hatched in laboratory, none seen in field); none recorded in 1952; August 1, 1953.

Numerous young that were only slightly larger than the one hatched in the laboratory, and one that was even smaller were recorded in late summer, before their first hibernations. These young were easily recognizable as hatchlings since the year-old young hatched the preceding summers had grown to many times the bulk of the hatchlings and in some instances, to more than twice their length.

In a hatchling captured on August 1, 1953, the coloration in life was as follows: entire dorsal surface jet black except for pale round or oval marks in three series on each side on certain cephalic plates, a median small faint one on dorsal part of rostral; a nearly round one in center of each supranasal covering about half of diameter of scale itself; somewhat oval one on each prefrontal, extending for length of scale (largest of markings on dorsal side of head); small faint one in each anterolateral corner of frontoparietal; small one in lateral portion of

each supraocular; nearly round one in anterolateral corner of each parietal almost as large as that on prefrontal; on each side one on dorsal part of first scale of third row (counting from mid-line) on neck.

These light marks are arranged in a linear series. On each of several anterior supralabials, one occupies most of the area, but on the large posterior supralabials they occupy only the central parts. Posteriorly, beyond the supralabials, this series is continued by a spot behind the ear opening which is approximately the size of the ear opening itself, and is the largest of all the light marks; one is on each of the first five infralabials, occupying most of each scale; one is on the median mental, one is on the median postmental and one is on each of the three chin shields on each side. Ventrally the body is slate colored. The tail is dark purplish blue.

Presumably the mortality is high among hatchlings. If this is so, the chances of recapturing any one individual after a period of months is poor. Only three individuals that were first captured and marked in late summer after hatching were recaptured as yearlings permitting tracing of their growth through and beyond the first year of life. Records of these individuals are shown in Table 4.

Hibernation lasts until late April or May and the smallest young taken in those months may not be much larger than hatching size. By the end of May, however, all have grown to a snout-vent length of more than 50 mm. June was the only month of the skinks' active season in which no young shorter than 50 mm in snout-vent length was taken.

By the time of emergence from the first hibernation, the young, although still small, may have begun change of the jet black color of the hatchling to the dull speckled adult pattern. In a juvenile of 57 mm snout-vent length, and weighing three grams, the color in life on April 2, 1953 follows: dorsal ground

TABLE 3. Sizes of young *Eumeces obsoletus* recorded before their first hibernations.

Date	Snout-vent length in mm.	Tail length in mm.	Weight in grams
July 25, 1949.....	40	50	1.1
July 31, 1949.....	39	49½	
August 1, 1953.....	39	51	
August 2, 1949.....	38	51	
August 2, 1949.....	39	39-1	
August 8, 1949.....	43	20*	
August 8, 1949.....	44	41½*	
August 8, 1949.....	43½	55	
August 13, 1949.....	45	62	
August 17, 1953.....	45	61	
August 17, 1953.....	50	65	.8
August 19, 1949.....	50	64	
August 19, 1949.....	46	55	
August 22, 1949.....	45½	20-12	
August 29, 1949.....	61	92	
August 20, 1950.....	36½	46	
August 23, 1950.....	43	54	
August 25, 1950.....	42	54	
August 28, 1950.....	36	44	
August 31, 1950.....	42	9*	
September 1, 1949.....	52	71	.5
September 2, 1950.....	32	39	
September 2, 1950.....	43	45*	
September 8, 1950.....	39	35½*	

\*Broken stub.

TABLE 4. Hatchlings recaptured in next two years.

Dates of capture	Snout-vent length in mm.	Tail length in mm.	Weight in grams	Remarks
Number 1				
Aug. 2, 1949....	38	51	5.4	Individual no. 1 was marked when it was a little larger than hatching size; subsequent growth up to an age of almost 23 months followed the trend shown in Table 8 but was consistently somewhat smaller.
June 21, 1950....	65	88	5.4	
Aug. 14, 1950....	83	120	10.3	
June 17, 1951....	86	59-66	11.5	
Number 2				
Aug. 19, 1949....	50	64	....	Individual no. 2 must have hatched in July 1949 as it was already well above hatching size when first captured on August 19. At first its growth was accelerated but it gradually lost this early advantage, and by the time of its last capture when it was approximately 22 months old it was slightly below average size for its age group.
Sept. 13, 1949....	59	34-2	....	
June 26, 1950....	77	49-39	7.7	
Aug. 20, 1950....	87	53-49	12.5	
May 21, 1951....	89	7*	10.3	
Number 3				
Aug. 29, 1949....	61	92	7	Individual no. 3 must have been at least a month old when first captured as it was already much larger than hatching size. At an age of two years it was still somewhat under small-adult size, and was about average length for its age group.
May 30, 1950....	65	87*	5.1	
June 21, 1951....	96	142	18	
July 21, 1951....	97	70-3	12	

\*Broken stub.



color mainly golden brown, but with each scale heavily edged with black; this black edging heaviest on the sides just above the level of the limb insertions, imparting the effect of a faint dark lateral stripe; below this dark lateral area at the level of the limb insertions, the dark edges are lacking, and there is a faint reddish suffusion about five scale rows wide. The ventral surface is silvery gray with a faint greenish suffusion; the dorsal and ventral color patterns of the body continue onto the limbs, which are a little darker than the body; the eye is dark. As in hatchlings, the labials are mainly white, with dark edges that are wider in the posterior ones, and there are orange marks on top of the head on each side. Otherwise the top of the head approximates the dorsal body color, but with more dusky suffusion. Lateral portions of the parietals are black. Both dorsally and ventrally the body coloration is continued onto the basal two-fifths of the tail. Farther posteriorly the tail becomes increasingly suffused with purplish blue.

There is a great deal of individual variation and probably geographic variation in the rate of pattern metamorphosis. Although the one described above may be fairly typical, others retain the black dorsal color longer, or lose it sooner. Cliff (1953) briefly described a young specimen of only 54 mm from Guasabas, Sonora, in which the coloration was uniform brown above except for the pale markings on the head. On the other hand, a yearling caught repeatedly on the Reservation in July and August, 1953, when it was nearing adult size (93 mm snout-vent length) still had the black of the hatchling pattern predominating (Fig. 9). Most year-old young have a pattern transitional between the patterns of hatchling and adult, but sufficiently different from either that all three sizes might be mistaken for different kinds. The effect is that of a faintly banded pattern. In a skink of 86 mm snout-vent length examined on July 14, 1953, the transitional color pattern was as follows: The four mid-dorsal scale rows form a band of coppery brown, with a narrow black edge on each scale. The line of contact between the second and third scale row on each side is black, forming an irregular stripe which averages approximately 0.5 mm in width. The remainder of the third scale row and most of the fourth together form a pale dorsolateral stripe. A dark lateral area approximately 2 mm wide occupies most of the fifth and sixth rows, which are mostly black with pale centers. For the width of approximately three scales below this dark area and down to the limb insertions, black pigment is lacking and there is a series of small irregular red blotches. This area is, however, not entirely distinct from the dark lateral area which has many red scales. The several longitudinal bands are not sharply defined, but blend into each other more or less. The ventral surface is silvery gray with a faintly yellowish suffusion. On the tail the dorsal stripes fade into each other and lose their identity. On the dorsal half of the tail each scale has a heavy black edge. Ventrally the tail has no dark markings.

Except on its basal fourth the tail has a faint bluish suffusion dorsally, and this suffusion extends onto the ventral surface near the tip. On the head the light spots of the hatchling pattern are retained, but they have become dull and less sharply defined. The cheeks are dark. There are irregular black markings on the edges or corners of each of the cephalic plates.

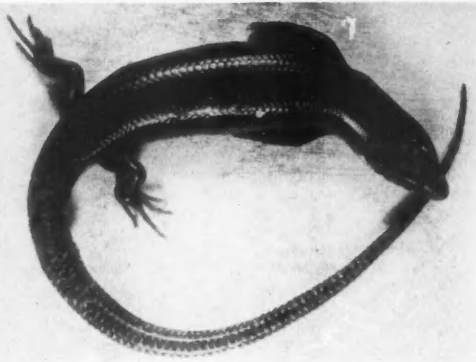


FIG. 9. Juvenile approximately the same age as the one in FIG. 10, and grown to slightly larger size, but exceptional in retaining to a large extent the dark pigmentation of the hatchling pattern;  $\frac{3}{4}$  natural size.

The Great Plains skink seems to have been derived from an ancestral form having a lined pattern, like that of its nearest relatives, i.e., *E. chinensis*, *E. kishinouyei*, *E. coreensis* and the five-lined skinks. In the juvenal *obsoletus* dark pigmentation has completely obscured the dorsal stripes except their fragmented anterior ends, represented by the series of pale spots on the head. In the adult the striped pattern is entirely lost. It is only in the half-grown young that the lined pattern is discernible, and even at this stage it is faint (Fig. 10).

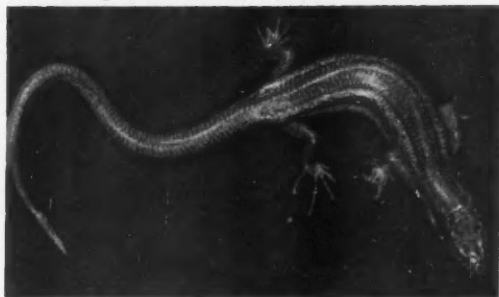


FIG. 10. Juvenile approximately one year old, with color and pattern almost like that of the adult, but showing faint stripes characteristic of this stage of development;  $\frac{5}{8}$  natural size.

In contrast to the individuals recorded in Tables 5 and 6 which mostly made steady growth in the intervals between successive captures, there were several seemingly stunted young, which although they were far short of adult size, grew only a little in long intervals between captures, or did not grow at all. These are recorded in Table 7.

TABLE 5. Growth within the skink's second growing season, following emergence from the first hibernation, as illustrated by the following records of four selected individuals.

Date and Number	Snout-vent length in mm	Tail length in mm	Weight in grams	Remarks
Number 1				
May 11, 1951....	49	24½-10	...	Like most others hatched in 1950 this individual was somewhat retarded as compared with young of 1949 on corresponding dates.
June 5, 1951....	55	30-16	...	
Number 2				
May 5, 1952....	52	71	...	This individual followed the general trend of growth but was a little behind the average.
July 1, 1952....	72	102	4	
July 15, 1952....	75	105	6.1	
Number 3				
May 15, 1950....	55	76½	3.2	This individual followed the typical growth pattern but was slightly below average size at each capture.
May 28, 1950....	57½	79½	...	
July 23, 1950....	77	113	9.6	
Aug. 25, 1950....	80	119	9.8	
Number 4				
June 16, 1949....	67	38*	...	At the time of its first capture when approximately 11 months old, this young was a little below average size but during the next two months it made unusually rapid growth and by late summer it was larger than average size.
Aug. 8, 1949....	94	58-62	17	
Aug. 22, 1949....	98	59-68	20	

\*Broken stub.

The skinks upon which Table 8 is based were all marked individuals from the study area whose histories were known more or less. In order to estimate the ages of the larger young (those more than a year old) with any degree of assurance, it was necessary to have the records of growth from the smaller sizes of the first year young. From the data in Table 8 it seems that typically, at least in females, sexual maturity is not attained until the skink is three years old. The smallest female found to have maturing ova had a snout-vent length of 107 mm which is approximately the average size of three-year-old individuals.

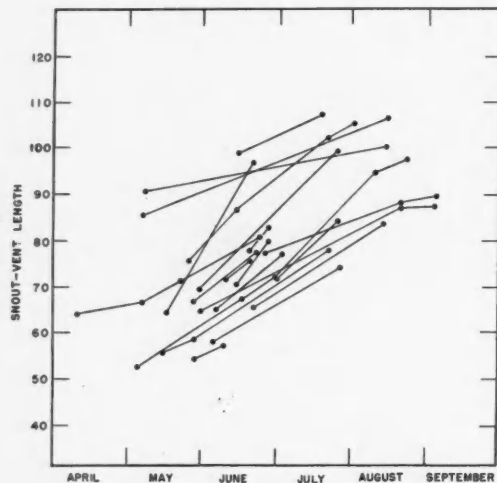


FIG. 11. Growth in snout-vent length in young Great Plains skinks taken two or more times within the same growing season.

The most notable fact concerning the growth of young is the great difference in rate between individuals of the same size. Some remain static for periods of months, while others continue their early rapid growth until they have reached nearly adult size. In other reptiles also (for instance in the rattlesnake, *Crotalus viridis*) many of the less vigorous or less fortunate young are stunted in their growth and never reach maturity. The records of such retarded individuals may give an erroneous impression of the time required to grow to adult size (Fitch 1949).

#### FOOD HABITS

Several authors have made casual observations concerning the food habits of the Great Plains skink. Grant (1927) kept a juvenile five inches long and recorded that it greedily ate small crickets, young grasshoppers, sow bugs, and freshly laid grasshopper eggs. Describing its actions in catching the prey he wrote: "... the lizard got his eye on the hopper and raised high his blue tail and waved it rapidly and gracefully making letter S's and then pounced on and devoured the small hopper. The tail waving seemed to serve as a distraction from the real danger, like the nervousness inherent in the end of a cat's tail." Hartman (1906) stated that this skink will attack animals as large as itself. One, that he kept, seized by the neck a hog-nosed snake a foot long, and shook it, attempting to kill it until forced to release its hold. This attack probably was motivated by a natural hostility to snakes and by self-defense rather than by an attempt to obtain food. Another skink killed and ate a young collared lizard three inches long. Stomach contents that Hartman examined contained large grasshoppers and crickets, and one skink had eaten a large ground spider. The stomach of a juvenile contained a fly, a grasshopper, two leafhoppers and a cricket. Young kept by Hartman in captivity injured or killed young *Sceloporus*

TABLE 6. Free-living skinks of adult or nearly adult size originally captured and marked in a previous year when so small as to be assignable to the brood of a particular year.

Date and Number	Snout-vent length in mm	Tail length in mm	Weight in grams	Remarks
Number 1				
May 26, 1949....	67	91	7	Must have been approximately 10 months old at time of original capture. Both on this occasion and at recapture more than a year later it approximated average size for its age.
June 3, 1950....	95	105-24½	18.1	
Number 2				
May 30, 1949....	67	91	9	About average size for its age (10 months) at original capture; continued rapid growth through the next two months but lost weight and gained but little in length in next 9½ months.
July 25, 1949....	99	144	21	
May 11, 1950....	100	152½	15.8	
Number 3				
June 6, 1949....	64½	102½	8	Approximated the average size for its age group in all three of its records, extending over nearly a year.
July 1, 1949....	76	116	....	
May 20, 1950....	94	141	17.9	
Number 4				
June 14, 1949....	72	99	....	Female first recorded as a half-grown young about 11 months old; not recaptured until four years old and near maximum adult size.
July 26, 1952....	123	93-40	....	
Number 5				
June 29, 1949....	78	91-11	11	Female first recorded at an age of about eleven months; recaptured at 35 months, grown to large adult size.
July 25, 1949....	87	98-15½	11	
June 11, 1951....	117	103-41	34	
Number 6				
Aug. 8, 1949....	44	41½*	....	Female hatched in July 1949 and first captured when only a few weeks old; recaptured as medium-sized adult near end of third year.
June 20, 1952....	112	122-33	....	
Number 7				
Aug. 16, 1949....	84	117	....	First captured at probable age of one year; still near minimum adult size when recaptured at 46 months.
June 23, 1952....	108	94-14½-1½	....	
Number 8				
Aug. 29, 1949....	94	139	20	Male, may have been either one year old or two when first recorded late in the summer of 1949; had attained small adult size when recaptured almost a year later.
Aug. 8, 1950....	108	160†	28.0	
Number 9				
May 9, 1950....	56	78	3.3	First recorded soon after emergence from its first hibernation; approximated average growth rate in ensuing year.
May 14, 1951....	88	130	14	
Number 10				
May 16, 1950....	65	93	5.3	First recorded soon after emergence from first hibernation, then slightly accelerated; 14 months later was still slightly larger than the average size for its age.
July 18, 1951....	98	151	22	
Number 11				
July 7, 1950....	82	88-25	11.1	First recorded at probable age of 11 months; made steady growth to near average adult size two years later.
May 31, 1952....	105	107-35	20	
July 6, 1952....	116	123-37	31.2	
Number 12				
June 3, 1950....	99	57-56	17.2	Male first captured as a well grown young either late in second year or perhaps in third year; 15 months later had grown to a medium-small adult.
Aug. 28, 1951....	112	66-63	24	
Number 13				
July 27, 1950....	70	100	6.0	First captured at age near one year; illustrates extreme retardation; had made so little growth when recaptured a year later that size was then typical of those only half its age.
July 18, 1951....	84	33-41	12.0	
Number 14				
July 28, 1950....	83	45-61½	10.7	First recorded at probable age of one year; just short of small adult size when recaptured 12½ months later.
May 7, 1951....	85	46-59	14	
Aug. 15, 1951....	106	127†	28	
Number 15				
July 19, 1953....	89	139	18.0	First recorded when a little less than one year old; well short of adult size when recaptured 11 months later.
Aug. 10, 1953....	97	62-4	19	
June 24, 1954....	103	70-50	25.2	

\*Broken stub. †Regenerated.

TABLE 7. Free-living skinks more than one year old that did not grow as expected.

Date and Number	Snout-vent length in mm	Tail length in mm	Weight in grams	Remarks
Number 1				
July 16, 1949....	84	60-45	12	About half grown when first captured; remained almost static for the next 11 months.
June 17, 1950....	86	60-48	12.7	
Number 2				
July 19, 1949....	95	145	20	Approaching adult size, in ten months made only slight gain in length and lost 32% of its weight.
July 25, 1949....	97	150	25	
May 17, 1950....	101	145	17	
Number 3				
July 31, 1949....	92	128-3	19	Near adult size, in ten months failed to gain in length and lost 27% of its weight.
Oct. 10, 1949....	92	124*	15.2	
May 28, 1950....	92	77*	13.8	
Number 4				
Aug. 14, 1950....	83	120	10.3	In ten months, made almost negligible gain in length and weight.
June 7, 1951....	87	59-66	11.5	
Number 5				
Aug. 16, 1949....	97	34-82	20	Approaching small adult size at time of first capture; made such slow growth subsequently that it was still near minimum adult size 24 months later; lost one-third of its weight in second year.
Aug. 1, 1950....	104	41-88	25.9	
Aug. 31, 1951....	109	59-2	16.7	
Number 6				
June 29, 1951....	95	113†	22	Negligible gain in length and no gain in weight in nine months.
April 2, 1952....	99	143†	21.2	

\*Broken stub. †Regenerated.

TABLE 8. Trend of growth in young Great Plains skinks.

Month	Probable age	Number in sample	Snout-vent length (average and extremes)	Weight in grams (average and extremes)
August.....	1 month	14	43.8 (61-36)	1.2 (1.7-8)
May.....	9½ months	17	59.3 (75-47)	5.7 (11-3.2)
June.....	10½ months	30	75.6 (99-55)	10.1 (22-2.8)
July.....	11½ months	29	82.7 (102-70)	9.2 (27-6.1)
August.....	12½ months	24	86.8 (99-71)	13.1 (20-5.2)
September....	13½ months	9	87.5 (97-78)	13.2 (21-8.8)
Apr.-May and June.....	20-23 months	19	92.3 (105-85)	16.0 (28-10.3)
July-Aug.....	23-25 months	5	96.6 (106-84)	18.4 (28-12)
May-Aug.....	33-37 months	9	106.5 (116-88)	

that were confined with them. Little & Elbert (1937) examined stomach contents of three specimens collected in New Mexico, which included a spider, fragments of a beetle, and remains of small insects. Burt (1928a) examined contents of three stomachs; one grasshopper (*Melanoplus*) and one katydid together made up 42%; three caterpillars made up 57%; and one spider made up one per cent. He quoted Taylor (MS) regarding the young which were observed to stalk slowly and craftily in approaching flies, catching them with sudden lunges. They were stated to pay no attention to dead or motionless objects. Burt & Hoyle (1934) recorded one taken in Morris County, Kansas, on May 14, 1933, which contained in its stomach an adult prairie skink (*Eumeces septentrionalis*). Burt (1928b) mentioned predation on caterpillars, grasshoppers, and moths. He observed

a large male (presumably in captivity) devouring a recently laid egg of the same species.

Much of the food probably is found in the sheltered situations where the skinks tend to stay. The extensive burrow systems that are excavated and then soon deserted may be primarily for the purpose of finding subterranean prey. Most of the recorded prey animals are of kinds which might be found underground in the places where the skinks burrow, and some are so swift when they are in the open that they would be likely to escape.

I cannot agree with the statement that the skinks pay no attention to dead or motionless objects. On the contrary, captives relied to a great extent on scent to find their food. When they were hungry, they would almost invariably accept as food meat held out to them on the end of a stick, unless they were frightened by my movements. They would first test the morsel with a single touch of the tongue, then immediately recognizing it as food, they would grasp it in the jaws. Live insects, spiders, and other prey introduced into the containers with captive skinks were usually soon recognized as food even though they remained motionless. Evidently sight played some part at least in attracting attention of the skinks, but invariably the object was touched with the tongue for olfactory test before it was actually grasped.

Observations on numerous captive skinks kept over periods of weeks or months, indicate that this species is less inclined to prey on small vertebrates than records in the literature would seem to suggest. On

many occasions I have kept other smaller lizards, especially five-lined skinks, with Great Plains skinks which, to my knowledge, never molested them. In one instance, several Great Plains skinks were kept in the same terrarium with incubating clutches of *E. fasciatus*. None of the eggs was eaten, and when the young lizards had emerged, these too were ignored by the Great Plains skinks, although the young were approximately the same size as the normal prey. Spiders of somewhat greater bulk than the young *fasciatus*, when introduced into the terrarium, almost always stimulated the Great Plains skinks to immediate pursuit and capture within a few seconds after they moved, whereas the brightly colored hatchlings moved about with impunity. When captive Great Plains skinks that had become accustomed to a diet of raw meat and insects were offered live newborn mice, they evinced but little interest. After the mice had been left for several hours in the container, they were found to be lacerated as if from bites, but none was eaten.

In the present study, items of prey were recovered both from stomachs of specimens dissected and from feces. The combined sample representing 113 meals with 217 identified items (Table 9) is a substantially larger sample than that provided by the records hitherto published. The items from stomachs were less fragmentary than those from the "seats", but all of the items had been more or less crushed, broken and digested, and identification to species was rarely

possible. The specimens providing the stomach items were from Douglas County at Pleasant Grove (6), and Jefferson County line west of the Reservation (6); Jefferson County on the section adjoining the Reservation to the north (5), and four miles north of the Reservation (4); Anderson County, four miles south of Garnett (4) and four miles southwest of Garnett (5); and Wabaunsee County, four miles north of Alma (3), one mile north of Alta Vista (1), and five miles southwest of Eskridge (10). All were collected in May and June.

The seats all were collected from June to September, and thus represent, on the average, a later stage of the season than do the stomach contents. Possibly some of the arthropods found in seats were first caught in the funnel traps and subsequently eaten there by captured skinks. Camel crickets and grasshoppers especially, were caught in large numbers in the funnel traps, and were better represented among the seat items than among the stomach items. The seats were obtained chiefly from the skinks caught at Rat Ledge and the quarry, and a few other places on the Reservation, representing areas of only a few acres, whereas those collected for stomachs came from numerous localities representing a variety of habitat conditions within a 40-mile radius.

The prey items included a variety of small animals. However the size range of prey is not great, as no items too large to be swallowed whole are taken, and the smaller items are of a size sufficiently large to provide a substantial mouthful. Three or four prey animals of average size ordinarily fill the stomach to near its capacity. The maximum number of separate items found in a stomach was nine. Another stomach contained eight items, two others each had six, one had five, two had four, five had three, nine had two, and the remaining 23 each had only one. In those that contained more than one item there was a marked tendency to take the same kind of prey repeatedly. For example, one had eight camel crickets, one had six *Phidippus audax*, one had four carabid beetles of the same kind. This may reflect merely availability at the time and place of foraging, but probably it indicates also individual preference. Such preference was evident in the feeding of captives.

The beetles eaten were of many different kinds, of several families, but carabids were those most frequently found. Scarabaeids were probably second in frequency. However, the larger members of this group, including the abundant "June bugs" are too bulky and heavily armored to be eaten ordinarily.

Orthoptera made up a little more than 32% of the food, in frequency of occurrence, and probably a considerably higher proportion of the total bulk. Camel crickets (*Ceuthophilus*) made up a greater part of the food than animals of any other genus. Probably most of them were of the same species. The grasshoppers included both nymphs and adults of several common species. A single grouse locust was recorded.

Spiders, making up approximately 24% of the

TABLE 9. Food items of Great Plains skinks, from contents of 44 stomachs and 69 seats.

	Frequency in stomach items	Frequency in seat items	Percentage of total occurrences
Orthopteran			
ceuthophilid.....	9	17	12.9
gryllid.....	5	12	7.8
grasshopper.....	7	17	11.0
miscellaneous.....	1	3	1.4
Coleopteran			
adult.....	24	15	18.0
larva.....	2	1	1.4
Spider			
Phidippus and other			
salticid.....	9	11	9.2
Lycosa.....	10	13	10.6
miscellaneous.....	3	6	4.1
Lepidopteran			
adult.....	1	—	.5
larva.....	12	—	5.5
Hemipteran.....	5	1	2.8
Ant.....	..	2	.9
Snail or slug.....	7	4	5.1
Miscellaneous insect.....	..	3	1.4
Skink.....	..	3	1.4
Sloughed skin.....	..	3	1.4
Phalangid.....	3	4	3.2
Miscellaneous larva.....	3	2	2.3
Total.....	100	117	100.0



total number of items, were chiefly of the genera *Phidippus* (especially *P. audax*, the common black jumping spider, with 16 occurrences) and *Lycosa*. Spiders of the former genus are commonly found on exposed rock surfaces and climbing on low vegetation. The wolf spiders are chiefly ground dwellers. Several were definitely identified as *L. rabida*, a common large grassland species, and one as *L. aspersa*. One small jumping spider was tentatively identified as *Habronattus viridipes*, a rock-dwelling species. Although most of the spider material could not be identified, all of it probably belonged to either the Salticidae or the Lycosidae.

The caterpillars found were probably of several different families. Some were spiny or hairy; others were smooth-bodied. They were up to an inch in length. Because of the lack of hard parts identification was especially difficult. Such larvae were not found in the seats, and probably no recognizable parts would have been available even if the skinks had eaten them. Only the most heavily chitinized parts of insects were intact in the seats.

Of the hemipterans found four were reduviids, all tentatively identified as *Melanolestes* or a related genus. The snails included two *Hawaiiia minuscula*, one *Gastrocopta armifera*, one *Stenotrema monodon*, one slug (*Deroceras*) and others too well digested to be identified.

In three instances bone fragments, osteoderms, and scales of small skinks, probably *Eumeces fasciatus*, were found, and these were the only remains of vertebrates.

Three phalangids were found in two stomachs and four in one seat. In captivity Great Plains skinks nearly always ignored phalangids, which usually were taken by five-lined skinks in the same containers. On several occasions an attacking skink was seen to release the phalangid and wipe its jaws vigorously against nearby objects, registering strong distaste.

Various small animals common or abundant in the situations where the skinks occur, but having noxious defensive secretions, or venomous stings or bites (centipedes, millipedes, scorpions, wasps) were not found in the food sample.

Insofar as could be determined the young and adults are similar in feeding habits. The young, of course, take smaller prey, but in many instances these are the same species that are preyed upon by the adults, or at least they are the same general type of prey. The diet probably changes in the course of a season. Most of the invertebrates preyed upon have an annual cycle of growth, reproduction and death, so that they are not equally abundant or available at all stages of the season. The data, however, are inadequate to show such seasonal changes.

### PREDATION

Burt (1933) recorded that one of these skinks was eaten by a collared lizard (*Crotaphytus collaris*) in captivity. The writer has found no other published record of predation on *E. obsoletus*. On August 30,

1948, at the northwest corner of the Reservation, a sudden movement in grass near the limestone ledge attracted attention to an adult blue-racer (*Coluber constrictor*) which had caught a large Great Plains skink. The skink, grasped by one flank, had twisted back and seized the skin of the snake's neck in a bulldog grip, and they lay interlocked, motionless except for their rapid panting and occasional straining of the skink to bite harder or of the racer to shift its grip and work its jaws toward the skink's head. The racer broke the skink's grip and began to swallow it head first. When only the hind legs and tail of the skink still protruded from the snake's mouth, I lunged forward in an attempt to catch both reptiles. With a sudden movement the snake disgorged the skink, which darted away into the grass and escaped. A juvenile blue-racer caught on September 17, 1950, had a Great Plains skink hatchling, partly digested in its stomach.

A recently captured king snake (*Lampropeltis calligaster*) to which a Great Plains skink was offered, instantly became alert, moved toward the skink stealthily, and suddenly seized it, enveloping it in constricting coils.

These skinks, when grasped, invariably attempt to bite the captor, at the same time squirming vigorously. One may twist its body, rotating the hind-quarters as much as 90° on the longitudinal axis, at the same time flexing the body laterally. The skink may defecate, pressing the anal region against the captor with a lateral motion which serves to spread the excreta, and probably increases their effectiveness as a repellent. This defense reaction is, of course, common to many other kinds of lizards and snakes.

Smith (1946) has described the defensive behavior: "Sonoran skinks are among the most vicious lizards of the country. They do not tame well and are likely to snap at almost any time. The bite is rather painful, for the small pointed mouth grabs only a small piece of skin and the jaws are extraordinarily powerful. With a piece of skin in its mouth, the skink hangs on a few seconds even if allowed to dangle free, and loosens its hold only after giving a final hard pinch and wriggling energetically. If they are forcibly removed they attempt to twist free and cause a very painful laceration."

Various snakes probably are among the chief predators on this skink, finding it in its hiding places, where it has little opportunity to escape by fleeing. Under such circumstances, the vigorous defense reactions noted, seizing the predator and biting hard and persistently, with the body held twisted and rigid, would seem to provide effective hindrance to swallowing.

Among 70 prey items recorded in a broad-winged hawk (*Buteo platypterus*) nest on the Reservation in June and early July 1954, there were six Great Plains skinks, all but one of which were adults and subadults. The nest was checked several times daily. All the skinks were caught in the mid-day hours whereas some other kinds of prey were caught most

often in early morning or late afternoon. The parent hawks had killed each skink with a bite through the back of the neck.

Small mammalian predators, especially those with the habit of digging out their prey, are important natural enemies. At Rat Ledge, opossums (*Didelphis marsupialis*), spotted skunks (*Spilogale interrupta*) and striped skunks (*Mephitis mephitis*) foraged regularly, and all of them occasionally attacked Great Plains skinks that were confined in wire funnel traps, and also almost certainly preyed upon them naturally. Although the traps were anchored down with heavy rocks to prevent such raids, the predators sometimes tore out the funnels to gain entry or tore the traps loose and rolled them down the steep slope, often without succeeding in opening them. Often the identity of the predator could not be determined, but on many occasions tufts of hair snagged on sharp projecting wires served to incriminate either an opossum or a skunk or a raccoon. On one occasion a trap that had been rolled several yards by an opossum contained a Great Plains skink that had lost many of its toes. Evidently the opossum had bitten off all the toes projecting through the quarter-inch wire mesh. On another occasion remains of a large skink were found partly eaten beside a trap which had been broken open and which bore signs of spotted skunk. Frequently scratching and digging in loose soil at edges of rock outcrops and boulders were noticed where the predators evidently had searched for food, in the situations utilized by the skinks. Ordinarily no distinct tracks could be made out to determine the predator's identity, but those of both kinds of skunks, and of opossums and raccoons were occasionally identifiable. In their raids on the traps, and in digging under rocks these animals seemingly were attracted by large insects such as *Ceuthophilus*, in some cases, at least.

The common mole (*Scalopus aquaticus*) often occurs in the same habitat with the Great Plains skink, at least in the area where field work was done, and it may be an important natural enemy. Frequently I noticed burrows of both mole and skink under the same boulder. On one occasion I kept an adult mole in captivity for several days and fed it exclusively upon the carcasses of a series of Great Plains skinks that had been partly dissected. It accepted these avidly, and seemed to thrive on them. When one was placed on the soil surface in the mole's container, the mole would soon burrow up beneath it and pull it underground to feed upon it. The carcasses were eaten almost entire, but patches of the bony skin and the head and feet were generally discarded.

In the skinks examined, signs of old injuries, presumably made by predators, were frequent. In several, an entire foot was missing. These individuals did not seem to be seriously handicapped. Some of them were fat and in excellent condition. Such amputations were found much less frequently in the abundant five-lined skink on the same area, and have rarely been noted in any other kind of lizard.

Amputation probably occurs when a skink, in its burrow, is seized by a sharp-toothed predator such as a mole. The skink itself would aid in the amputation by its violent twisting and thrashing.

Several individuals had injuries of much different appearance, with lacerations of both dorsal and ventral surfaces. Such an injury might have been made by a snake attempting unsuccessfully to swallow the skink. The majority of individuals examined had regenerated tails. Although the tail may be broken by accident, most breaks occur when the skink is attacked by a predator. Probably the skink's life is often saved by the resulting distraction, as the predator pursues and eats the lively wriggling tail, permitting the less conspicuous and more elusive lizard to make its escape. The smallest skinks that I examined, up to 45 mm, all had complete tails when found, although in several instances I broke the tail in capturing the lizard. In the skinks of successively larger size groups the percentages retaining the original tail intact steadily decreased, as follows: snout-vent length 36-45 mm (14 skinks), 100% had intact tails; 46-55 mm (18), 83%; 56-65 mm (13), 69%; 66-75 mm (12), 58%; 76-85 mm (27), 41%; 86-95 mm (24), 33%; 96-105 mm (65), 28%; 106-115 mm (101), 31%; 116-125 mm (95), 23%; 126-135 mm (14), 14%.

Most adult skinks have scars on the dorsal surface or sides of the body or tail. On September 16, 1949, an adult found at the Quarry had its right shoulder and spinal column injured so that the back was kinked. Perhaps it had been bitten by a skunk or opossum. Scales were missing from the right side of the head and the chin was deeply gashed. This skink was caught three times within a week, late in the season when there is normally but little surface activity. It probably was unable to burrow because of its injuries. Its weight declined from 37 gm on August 13 (before the injury was received) to 20.7 gm on September 23, the last date of capture.

#### PARASITISM

Several of the Great Plains skinks dissected had numerous small white cysts of an unidentified parasite in their body cavities. One had an especially heavy infestation while others taken at the same time and place had none.

Skinks of this species are especially subject to chigger infestation. According to Mr. Richard B. Loomis, who has studied chigger distribution and hosts in the central United States, four species have been found on *E. obsoletus*. All are of the genus *Trombicula*, namely *T. gurneyi campestris* (in central Kansas and southwestern Oklahoma), *T. montanensis* (in west-central Kansas), and in eastern Kansas *T. (Eutrombicula) lipovskyana* and *T. (E.) alfreddugesi*. Although both the latter species were recorded on skinks from the Reservation, *T. (E.) alfreddugesi* was by far the more common. This abundant pest chigger is the one that normally infests humans in the United States. In April and May the skinks are ordinarily free of chiggers.

Earliest dates of infestation recorded on the Reservation were: June 6, 1949; June 4, 1950; June 11, 1951; June 12, 1952; June 17, 1953. Heaviest infestations occur in July and early August. The numbers attached to skinks rapidly decrease later in the summer; activity and reproduction of the chiggers is reduced in dry weather.

Typical infestations are illustrated by the 13 skinks caught on August 8, 1949. Eight that were adults and subadults had infestations of approximately 20, 25, 50, 60, 100, 200, 200, 200 and 25). A half-grown male had more than 100 and three hatchlings each had 30 to 40. In those having light infestations chiggers were concentrated chiefly at the leg insertions, especially the foreleg insertion.

Chiggers tend to attach in groups or clusters. The injury to the skin resulting from the attachment of one permits others to attach nearby until dozens are lodged together in a close packed mass. Especially favorable sites for attachment are where there are protecting folds, and where there are relatively large areas of exposed skin between the scales. The leg insertions, the sides of the neck and body, and the eyelids are common sites of attachment. In heavy infestations there may be hundreds of chiggers on a skink, with masses at each leg insertion, and with more or less continuous clusters along the sides of the neck and body, so densely packed beneath the edges of the scales that the scales stand out from the body. Even in such heavy infestations, the skinks suffer no obvious ill effects, and usually appear to be in good condition.

Compared with other reptiles in the same habitat, Great Plains skinks carry chiggers in relatively large numbers. On the Reservation the racerunner (*Cnemidophorus sexlineatus*) is the only other lizard that carries comparable numbers. On the five-lined skink the chiggers average only a small percentage of the numbers found on the Great Plains skink. The smaller size of the five-lined skink, and its preference for an open woodland habitat do not fully account for the difference in numbers of chiggers. When individuals of both species, of similar size, are caught at the same time and place, the Great Plains skinks usually have many more chiggers on them.

Whether the specific difference in susceptibility to chigger infestation is based upon physiological preference of the parasite or on difference in habits of the hosts is unknown. *E. fasciatus* is quicker, more active and less clumsy than is *obsoletus*. Individuals

of *fasciatus* moving about in the open are often noticed to scratch themselves, perhaps brushing off chiggers before they have had time to attach. Ring-necked snakes (*Diadophis punctatus*) and worm snakes (*Carphophis amoenus*) often found under the same rocks where Great Plains skinks stay, have never been found infested with chiggers.

In places of favorable habitat where the Great Plains skink population is high, it is probably one of the principal carriers of the common chigger, which however, utilizes a large number of alternative hosts, including species of reptiles, birds, and mammals, in a variety of habitat situations.

## NUMBERS

Adult males become active somewhat earlier in the season than do females. Of 19 adults and subadults collected off the Reservation in April in three different years, all were males and of 43 April captures on the study area, 32 were of males. Otherwise there is no obvious difference in seasonal trends of occurrence between the sexes, or between young and adults, in contrast to the condition in *Eumeces fasciatus*. A collection of 115 Great Plains skinks taken off the Reservation in the months of May, June, and early July consisted of 50 considered to be adults (26 males and 24 females), 107 mm or larger in snout-vent length; 44 considered to be two- or three-year-olds (23 males and 21 females), 77 to 106 mm in snout-vent length; and 21 yearlings.

At Rat Ledge during the five years that the study was in progress, the population underwent steady reduction, evidently as a result of deterioration of the habitat. Just how the reduction occurred is not entirely clear, but some of the skinks originally present were probably eliminated by normal mortality factors and others eventually dispersed as habitat conditions became less favorable. If they followed the ledge south a quarter of a mile to the Reservation boundary, they would have reached a heavily grazed, rocky, hillside pasture, which offered favorable habitat and was known to support a high population. Some probably migrated to this area, which also may have been the source of many individuals that appeared on the study area from time to time. The recorded population of Rat Ledge in each of the five years of the study is shown in Table 10.

In 1949 the species' biomass was calculated to amount to a little more than three-fourths of a pound

TABLE 10. Numbers of Great Plains skinks caught at Rat Ledge each year.

	Adult male	Adult female	Two-year-old and immature 3-year-old	Yearling	Hatchling	Total
1949.....	12 (all new)	11 (all new)	23 (all new)	18 (all new)	7	71
1950.....	16 (10 new)	10 (5 new)	16 (9 new)	26 (24 new)	2	70
1951.....	4 (3 new)	18 (9 new)	16 (7 new)	7 (all new)	none	45
1952.....	6 (none new)	8 (1 new)	1 (not new)	1 (new)	none	16
1953.....	5 (2 new)	2 (none new)	1 (not new)	5 (3 new)	2	15

per acre for Rat Woods, an area of a little more than four acres. This figure may be typical for the areas that provide favorable habitat, but certainly much higher population densities exist in unusually suitable habitat. Such optimum habitat is however usually limited to small areas of not more than a few acres in any one locality.

In the late summer of 1949, numerous hatchlings were seen along the ledge but in 1950 they were scarce, and none was seen in 1951 or 1952. The cool, wet summer of 1951 may have been especially unfavorable for development of the eggs as few young definitely assignable to the 1951 brood were recorded either on the Reservation or elsewhere. Heavy precipitation in 1951 hastened the process of succession, by which saplings, shrubs, and rank weedy vegetation encroached upon the formerly open areas along the ledge, rendering them less favorable habitat. In 1952 and 1953 the few adults captured were all individuals known to have been present on the area in previous years, and immature skinks were especially scarce.

In the five-year reduction from abundance to scarcity, one of most striking changes was that in the adult males, from the 16 recorded in 1950 to the four recorded in 1951. The more vagile males evidently shifted away from the area sooner as conditions became less favorable. The females actually seemed to increase in numbers from 1950 to 1951. As habitat conditions worsened, those in marginal situations may have retreated to the vicinity of the ledge before leaving the study area altogether. A similar but earlier temporary increase in males was noted from 1949 to 1950. Many of the adult skinks were taken only once, or were taken a few times at points that were relatively widely separated, suggesting that they were transients on the study area.

#### SUMMARY

Over a five-year period, 1949 to 1953 inclusive, at the University of Kansas Natural History Reservation, a population of Great Plains skinks was studied. Many of them were marked by toe-clipping, and individuals were recaptured as many as 17 times. These and others were observed under natural conditions, and from time to time individuals were kept in captivity to observe various phases of their life history.

The Great Plains skink is a prairie species thriving best in open situations with low vegetation. In this habitat preference it resembles its nearest relative *E. chinensis* of eastern Asia, but differs from various other less closely related skinks of the same genus. In its geographic range it overlaps eleven other species of the genus, none closely related to it or similar in habits. The study area, near the northeastern limit of the geographic range, was, under original conditions mainly open prairie, and much of it must have afforded favorable habitat. With the establishment and closing in of a deciduous forest type (as a result of control of prairie fires) the

skink's habitat shrank to the few remaining small open areas where heavy grazing had held back advance of the woodland. During the period of the study, plant succession on the Reservation, hastened by discontinuance of grazing in 1948, brought about changes unfavorable to the existence of the skinks, which by 1953 were reduced to a small fraction of their abundance in 1948.

Great Plains skinks breed in May, and in June or early July females produce clutches of 7 to 17 eggs. Productivity is low, however, as many adult females seem not to participate in the annual breeding season. The eggs are laid in damp soil, in nest burrows excavated by the female, usually beneath sunken boulders. The female guards her clutch which may require about seven weeks to hatch. The young, hatching in late July, or as late as September, differ strikingly from the adults in appearance, with black dorsal coloration, white and orange spots on the head, and bright blue tail. Young, 40 mm or less in snout-vent length at hatching, grow rapidly at first. After emergence from hibernation the following spring, their coloration gradually changes, so that at an age of a year most of them resemble adults in coloration more closely than they resemble hatchlings, but are still somewhat intermediate. The rate of growth is variable. Many young seem to be stunted, and for reasons that are not evident, they fail to make normal growth. Some individuals reach small adult size at an age of two years, but most require three years, and some others require even four years. At an age of four years some individuals have grown to nearly maximum adult size.

The Great Plains skink has an extensive geographic range. It invades habitats of both deciduous forests and deserts, but these occurrences are marginal. Most of its range is within the southern Great Plains, in an open and somewhat arid habitat, usually where grass and low, shrubby vegetation are present. It seems to be most abundant in the northeastern part of its range, notably in the Flint Hills of Kansas. Farther south and southwest it occurs mainly in rugged terrain, especially at higher altitudes, in canyons, mesas, and mountains. Lizards of this genus are especially subject to injury or death from desiccation. The Great Plains skink escapes desiccation by its fossorial habits, and spends most of its time in the burrows that it excavates. Various incipient adaptations to subterranean life are evident in the form of its head, body and limbs, but all these are minor in degree.

These skinks tend to be sedentary in habits and one may spend weeks in an area of only a few square yards. Although a skink may spend days or even weeks in the same burrow without emerging, this does not constitute a permanent home base, as the lizard will eventually move to another such burrow. Most shifts are short ones within an area familiar to the skink and constituting its home range. The skinks tend to occupy as home ranges areas of more than 50 ft. but less than 150 ft. in greatest diameter. Shifts to new home ranges occur from time to time.



Vagility is greater in males than in females and greater in adults than in young.

Food is found chiefly in the sheltered situations where the skinks stay, and both sight and scent are used to locate the prey. Unlike many lizards this skink readily recognizes as food edible objects that are motionless. Prey consists of many kinds of small invertebrates. Some of the more important groups are: beetles (chiefly carabids and scarabaeids), camel crickets, grasshoppers, crickets, ground living spiders, especially those of the genera *Lycosa* and *Phidippus*, caterpillars and snails. Occasionally small lizards including other species of *Eumeces* are eaten.

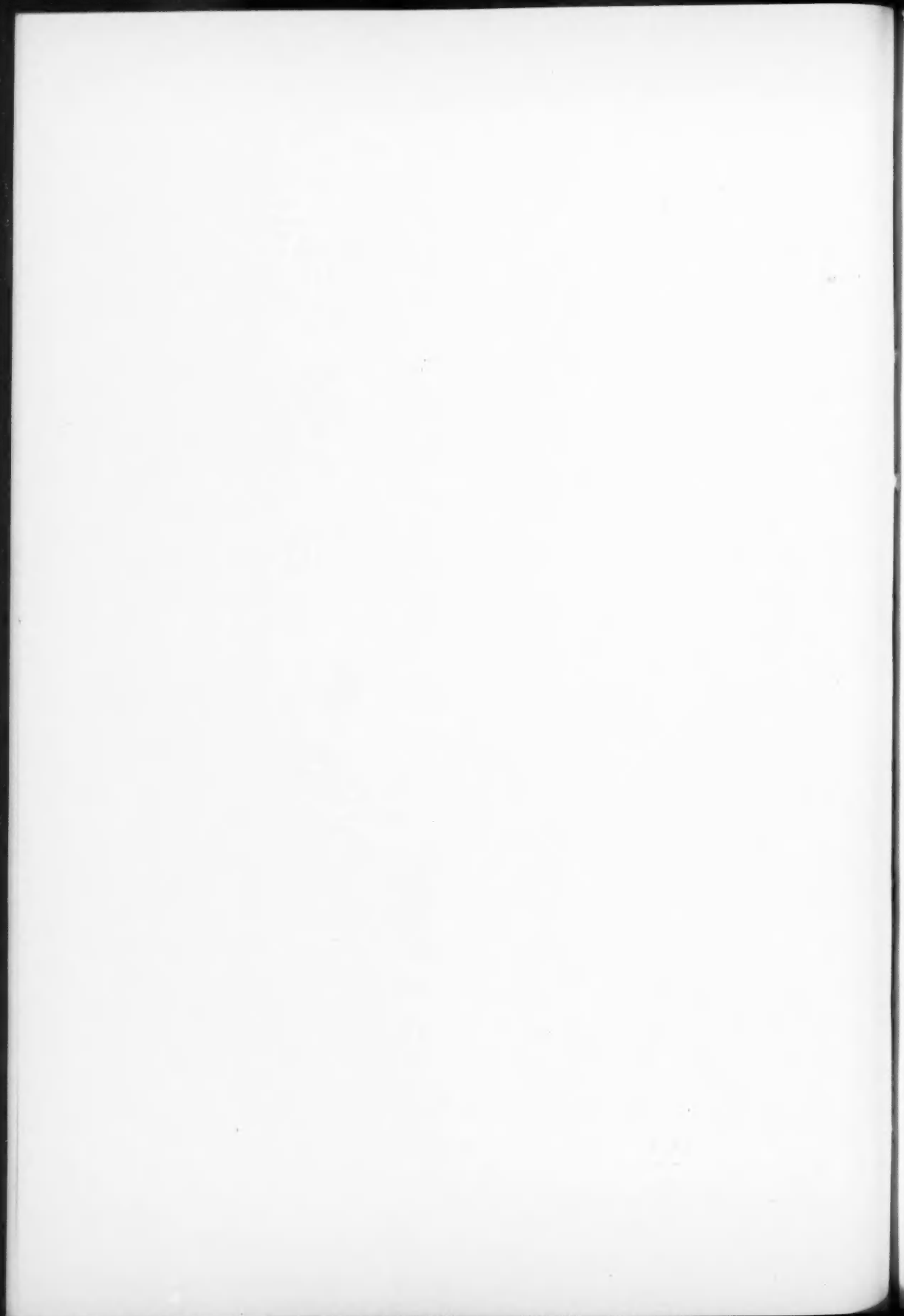
Predators on the Great Plains skink are known to include the collared lizard, blue-racer, broad-winged hawk, common mole, opossum, and spotted skunk. The fragile tail evidently serves frequently as a decoy to divert such enemies, for most adult skinks and the majority, even of the half-grown young, have had the tail broken and regenerated at least once. Although they are not especially swift these skinks rely on wary and elusive behavior to escape predators. When above ground they generally stay close to escape shelters and are alert to retreat into them at the slightest cause for alarm. When captured, they defend themselves with great vigor and are capable of inflicting a painful bite. As a secondary defense the skink defecates in such a manner as to smear its own body and that of the captor.

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# ECOLOGICAL RELATIONS OF JAEGER AND OWLS AS LEMMING PREDATORS NEAR BARROW, ALASKA

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## TABLE OF CONTENTS

	PAGE		PAGE
INTRODUCTION .....	85	Predation and food consumption .....	104
METHODS .....	86	MINOR PREDATORS .....	105
MAJOR PREDATORS .....	87	1. Long-tailed Jaeger .....	105
1. Pomarine Jaeger .....	87	2. Parasitic Jaeger .....	105
Relative numbers .....	88	3. Glaucous Gull .....	106
Nesting cycle .....	91	DISCUSSION .....	107
Territoriality .....	93	1. Timing of breeding effort in relation to breed-	
Predation and hunting behavior .....	96	ing success .....	107
Field use of plumage characters .....	97	2. General status in the arctic of avian predators	
2. Snowy Owl .....	98	near Barrow .....	108
Relative numbers .....	98	3. Interspecific relations and the fact of	
Nesting cycle .....	99	competition .....	111
Predation and food consumption .....	101	4. Predation in relation to population levels	
3. Short-eared Owl .....	102	of lemmings .....	113
Relative numbers .....	102	SUMMARY .....	115
Nesting cycle .....	103	LITERATURE CITED .....	116

## INTRODUCTION

Avian predators in the high arctic, as also the lemmings which support many of their breeding populations, are of special interest to population ecologists because of periodic fluctuations in their numbers. These are so violent and consistent, and the over-all picture is so diagrammatic, that the arctic seems to provide the best, if not the only situation which reasonably can be expected to reward those seeking to ascertain whether regular fluctuations in natural populations can be self-promoting (Solomon 1949). Since predator populations vary in accordance with those of the prey, the main objective of the work reported here was to record occurrence of avian predators near Barrow, Alaska, in the years 1951-53, to estimate their breeding densities, and to correlate these with lemming abundance. The species of chief interest were the pomarine jaeger, snowy owl, and short-eared owl. At the same time, it was possible to collect data on their breeding cycles and territorial behavior. On these topics we report those parts of our material relevant to the over-all picture of activity in populations depending on a common prey. Other aspects of behavior are dealt with elsewhere (Pitelka *et al.* 1955).

Evaluation of our observations from the standpoint of avian life-history and what little there is on eco-

logical relations has been greatly facilitated by such general works as those of Bent (1921, 1938), Withersby *et al.* (1940, 1941), Salomonsen (1951), and Dementiev *et al.* (1951). In addition, many original references have been examined; but from the point of view of population study, the literature offers very little. Many basic facts concerning the ecology and behavior of even the best known birds of the high arctic have yet to be recorded, and for such a widespread species as the pomarine jaeger, published information is scant. Of the persons who have had opportunities to record intensive observations in one arctic area over a period of years, most have been interested primarily in faunistics, at best including in their papers only scattered life-history information for as many species as possible. Among writers dealing with birds, Pleske (1928) appears to be the only one of the old-school faunists who attempted to extract and synthesize from his piles of records some data pertaining to a problem of biological interest, in this case the timing of breeding among high arctic birds.

In this paper we are attempting primarily to present data relevant to problems of predator-prey relations in general (Errington 1946) and the lemming cycle in particular (Elton 1942). We have included information on breeding and territorial be-

havior because the role of jaegers and owls as predators can hardly be properly assessed without knowledge of the main events of the nesting cycle, their timing, and population organization as these are manifest in a high arctic environment under given food conditions. Much of modern population ecology rests on factual, but critical natural history, and we have reported our original observations in detail when they are germane to one of the basic problems mentioned above.

What value our information on avian predators may have derives from the fact that the abundance of lemmings was different each summer of our field work, and an exceptional opportunity was provided to witness the occurrence and behavior of predator populations in the three contrasting seasons. Over the coastal plain of arctic Alaska, two species of lemmings occur, the brown (*Lemmus sibiricus*) and the collared (*Dicrostonyx torquatus*) (Rausch 1953). The latter species occurs only in moderate numbers. It is the brown lemming which becomes abundant at Barrow and undergoes violent cyclic fluctuations in numbers. In the course of the three years beginning in 1951, the population of brown lemmings passed through a cyclic rise, following a drop which occurred in the spring and early summer of 1949 and a low which continued through the summer of 1950 (Rausch 1950) and into 1951. Through 1952 and 1953 there was a dramatic upswing in numbers. During this period, the ecology of lemmings near Barrow was under study primarily by Daniel Q. Thompson, and background information on their populations will become available as forthcoming papers are published.

Four species of birds, already with fair to excellent reputations as predators of lemmings, nest near Barrow or at least occur there more or less regularly. These are the pomarine jaeger (or pomatorhine skua of European works), *Stercorarius pomarinus*; the parasitic jaeger (or arctic skua), *S. parasiticus* (formerly *S. crepidatus*); the long-tailed jaeger (or long-tailed skua, earlier called the Buffon skua), *S. longicaudus* (formerly *S. parasiticus*?); and the snowy owl, *Nyctea scandiaca*. (This enumeration of names is necessary to apprise the reader of the risks of confusion in the literature on lemming predators.) Two other species more or less innocent of such reputations but figuring in the picture of predation near Barrow are the short-eared owl (*Asio flammeus*) and the glaucous gull (*Larus hyperboreus*). Additional species known to prey on lemmings in other parts of the arctic either are unknown near Barrow (as the raven, *Corvus corax*) or occur there merely as vagrants (as the gyrfalcon, *Falco rusticolus*).

The research reported here represents one part of a program of studies on population biology of arctic land vertebrates conducted at the Arctic Research Laboratory, Point Barrow, Alaska, in 1951-53 under the auspices of the Office of Naval Research (contract N7onr-29542 with the University of California) and the Arctic Institute of North America. The financial aid provided by these agencies is gratefully

acknowledged. For facilities provided at the Arctic Research Laboratory, for generous assistance in many ways, and for friendly counsel, we are greatly indebted to its former director, Dr. Ira L. Wiggins. Observational records and specimens used in the preparation of this paper were collected in the field by the authors and by H. E. Childs, Jr., K. L. Dixon, G. W. Greenwald, P. D. Hurd, Jr., and W. L. Thompson. Their share in the accumulation of data was both considerable and effective. In the research upon which this paper is based, Tomich participated in 1953, Treichel in 1952. W. W. Dunmire helped in Berkeley with the organization of specimen data. For data on weights adding substantially to those collected by us, we are indebted to Brina Kessel (University of Alaska), R. W. Storer (University of Michigan), and Robert Rausch and Laurence Irving (both at the Arctic Health Research Center, Anchorage). With Dr. Rausch, also, we discussed many aspects of the biology of arctic mammals and birds; these occasions were always helpful and stimulating. O. J. Murie kindly provided records of Snowy Owl nests observed near Hooper Bay in 1924. Investigators and their staffs at the Arctic Research Laboratory, through their interest in birds and mammals, brought many items of information to our attention and assisted in various ways. All such help was much appreciated, and in conjunction with this report on avian predators, we would like particularly to thank P. H. Baldwin, M. C. Brewer, T. J. Cade, W. H. Craig, W. L. Groth, Jr., J. J. Koranda, G. E. MacGinitie, W. V. Mayer, S. J. Odend'hal, E. L. Schiller, H. W. Setzer, D. Q. Thompson, E. Wilhelm, and D. E. Wohlshlag. Also, we want to thank Tom Cade for the use of his excellent bibliography of Alaskan ornithology. Specimens have been examined in the collections of Stanford University Natural History Museum and the California Academy of Sciences through the kindness of their curators, G. S. Myers and R. T. Orr, respectively. R. L. Williamson and C. Roscheck assisted with translations of Russian and Scandinavian literature, respectively. A. H. Miller and O. P. Pearson read the manuscript critically and offered many helpful suggestions.

#### METHODS

Data on densities of jaegers and owls were obtained in two ways. First, an area of 9 sq. mi. in 1952 and a smaller one of 7 sq. mi. in 1953 were surveyed systematically for the location of breeding pairs. This was done using a vehicle (weasel) from which pairs and, during the incubation period, pomarine jaegers on eggs could be seen easily on the flat terrain of the Barrow area at distances of up to a half-mile; snowy owls could be seen even farther away. When a man or vehicle entered a territory, nesting jaegers habitually yelled and dived toward the intruder; and locally resident individuals were thus quickly detected. Locations of resident pairs and nests of all species were entered on a base map prepared from air photographs. Using the front of the weasel as a

lookout on which to stand, and with the aid of binoculars, the observer could plot pairs located around and near the weasel, then move to a new spot and repeat this, adding records of new pairs at the same time that locations of pairs seen earlier were double-checked. This survey was conducted on various dates from June 26 to July 23 in 1952 and from June 17 to July 15 in 1953.

In 1952, except for the southeast corner, the survey area was visited repeatedly, and error in total count of pomarine jaegers is considered to be not more than one or two pairs. In 1953, because of the great increase in density of jaegers, the area censused was smaller and outside of the four or so sq. mi. traversed frequently along various routes, an effort was made to check location of pairs at least twice in the nesting season. This was done on all except the peripheral parts of the survey area along the southern margin. The error in total population count of pomarine jaegers may be about 5%, but we believe it is not more than this. Numbers of breeding or locally established parasitic jaegers and snowy owls were small and satisfactorily determined. Short-eared owls, abundant in 1953, were not easy to locate systematically in the course of the general survey with the use of a weasel because incubating females sat closely, males spent relatively little time on wing, and usually neither took wing until man or vehicle was only a few feet away. The ground-resting owl was not only inconspicuous against the background of tundra vegetation, but males had the habit of squatting down and appressing themselves against the ground when approached, thus tending to resemble an incubating female and to hide themselves more effectively. Hence, although the map for 1953 (Fig. 4) shows all pairs located, there were many more. Breeding densities of this owl were determined satisfactorily only for the special census areas to be mentioned below and their immediate vicinities.

The second source of information on numbers of jaegers and owls was data obtained from areas censused intensively and periodically for total bird populations. The areas and coverages were as follows:

Year	PLOT 1 Old Beach Ridge 40 acres	PLOT 2 Low Tundra 20 acres	PLOT 3 Marsh Flat 86 acres
1951.....	June 10-July 15 (11 separate dates)	June 13-July 27 (9 separate dates)	June 27-July 16 (3 separate dates)
1952.....	June 11-July 12 (10 separate dates)	June 13-July 12 (8 separate dates)	June 26-July 17 (6 separate dates)
1953.....	June 5-July 8 (10 separate dates)	June 11-July 29 (12 separate dates)	June 19-July 26 (5 separate dates)

Details of censusing procedure are given elsewhere. Here the program of census work on three special areas is outlined sufficiently to show that for these we had a close knowledge of numbers of pomarine jaegers and short-eared owls and against this background, observations in the survey area were evaluated and interpreted.

For convenience in writing, we have chosen to refer to the larger areas as "survey" areas and the smaller ones as "census" areas. But it should be clear that

both are technically census areas since the results obtained (or at any rate the estimates sought) are numbers of birds of each species per unit area.

Finally, at all times other than those devoted to census or survey work, an effort was made to record significant observations of local occurrence, behavior, and seasonal change in activities of jaegers and owls. Nesting records and data on local numbers were also obtained on many trips 2 to 4 mi. south of Barrow Village and the Navy Base to the southwest of survey areas, on several trips in 1952 and 1953 to Ikroa-vik Lake 6 mi. south, and on one trip in 1953 to "Barrow-3" 10 mi. south. Recent records from other parts of the Alaskan arctic coastal plain obtained by our group or others working out of the Arctic Research Laboratory are mentioned when these supplement observations near Barrow.

### MAJOR PREDATORS

The various species of birds and mammals which prey on lemmings near Barrow, Alaska, are listed in Fig. 2. Certain prey relationships among the predators themselves, witnessed by us, are also shown there. The most important predators are the pomarine jaeger, snowy owl, short-eared owl, arctic fox (*Alopex lagopus*) and least weasel (*Mustela vison*). At least five additional species prey on lemmings near Barrow: red fox (*Vulpes fulva*), short-tailed weasel or ermine (*Mustela erminea*), parasitic jaeger, long-tailed jaeger, and glaucous gull. But these five are apparently only of minor importance because their populations are small (the first four) or because they are not habitually rodent predators (the gull). The foxes are present near the coast in numbers only in the winter. The short-tailed weasel was obtained by us only once, in June, 1953. Only the least weasel, of the mammalian predators, is important through the summer. Of the avian species, the three figuring among the major predators will be discussed first.

#### 1. POMARINE JAEGER

For all parts of the arctic for which observations from several years are available, the literature bears out a fluctuation in numbers of jaegers for each general area where two or three species of jaegers occur. The populations of the largest of them, the pomarine jaeger, appear to be as "mobile" as those of the two smaller species, and indeed year-to-year variation in numbers in any one area may even be greatest for the pomarine jaeger. This is suggested not only by the observations of individual writers, but even better by the experiences of different observers reporting on one general area. Again and again, from American as well as Eurasian sectors of the arctic, one writer tends to suggest that the other fellow might have been a little remiss in not finding jaegers as reported by the former. This preoccupation with faunistics and the assumption of earlier students of species distribution that a fair picture of constancy is easily forthcoming serve the happy purpose, for the arctic, of emphasizing the year-to-year



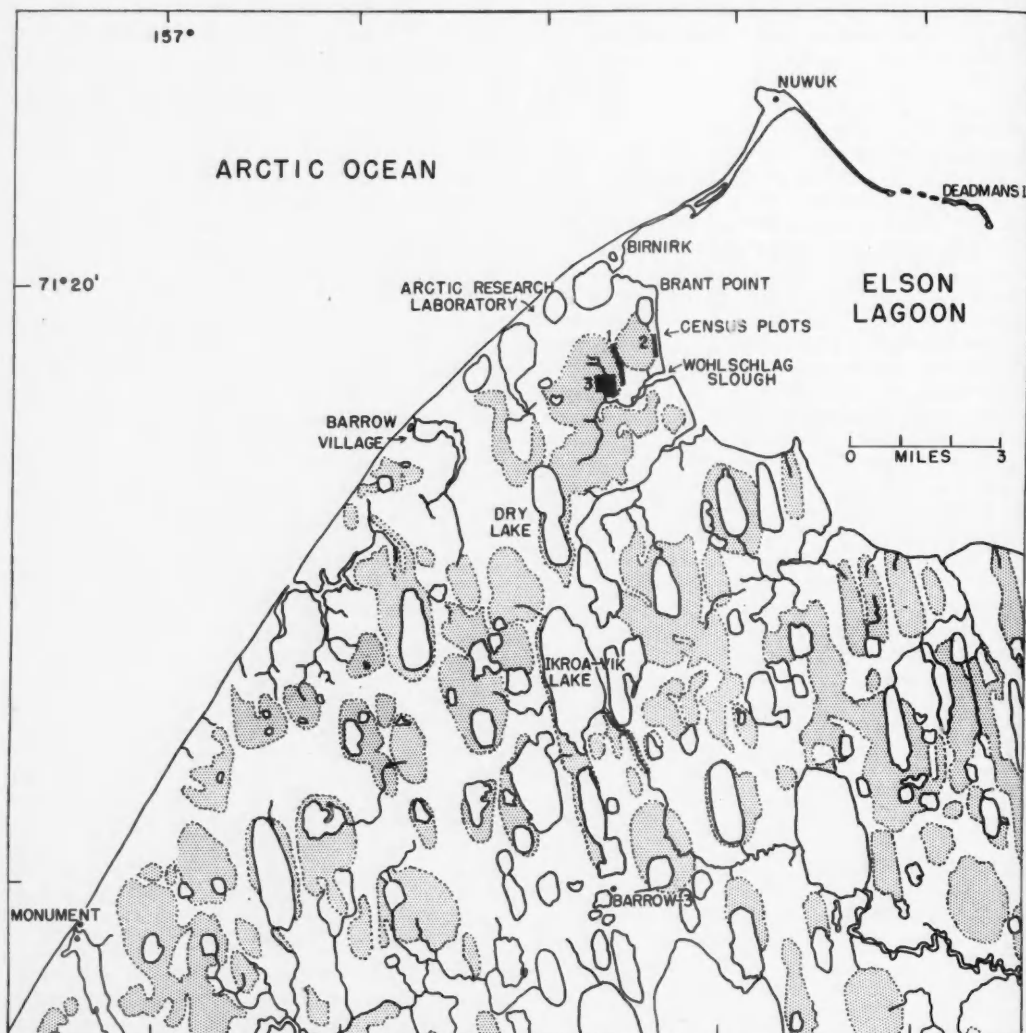


FIG. 1. Map of the area near Barrow, Alaska, showing localities mentioned in the text. In the shaded areas there are marshy flats, low-center polygons, and small ponds. Unshaded land areas represent higher, better-drained tundra.

contrasts which occur normally in the breeding distributions of many birds and particularly jaegers.

In the Barrow area (Bailey 1948), the pomarine jaeger is in general the most numerous of the three species and is abundant when lemmings are numerous. The statement of Southern (1944) that *parasiticus* "pushes out" *pomarinus* in arctic Alaska is clearly in error. For Point Barrow, Southern cites Anderson (1913, 1915), whose experience in finding few pomarine jaegers correlates with the fact that he did not find lemmings anywhere numerous, as is indicated in Anderson's 1913 paper.

Pomarine jaegers may occur from late May to early September. Extreme dates recorded by McIlhenny (Stone 1900) in 1897-98, when pomarine jaegers were

abundant and nested, are May 23 and September 20, and this period includes almost all other records. These two years were apparently comparable to 1952-53 with respect to phase of the lemming cycle. Lemmings support the breeding population, and pairs of jaegers scatter themselves out over the tundra on mutually exclusive, all-purpose territories.

*Relative numbers.* In the spring of 1949, at the time of a die-off following a lemming peak (Rausch 1950), jaegers were present on May 6 and estimated at 30-40 individuals per square mile. All of eight killed that day had been feeding on Lemmus. Later, on May 29, both jaegers and owls were abundant. Jaegers nested near Barrow, and perhaps also at least an occasional pair of snowy owls (see record

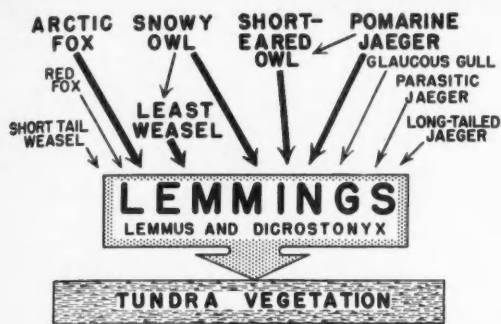


FIG. 2. Bird and mammal predators exploiting populations of lemmings near Barrow, Alaska; names of the most important species are shown in bold letters.

under latter species). In the spring of 1950, on May 29, jaegers were absent on the tundra, but a few were observed on the 30th migrating along the open lead well offshore. On the 31st, in the course of a ten-mile trip south and southwest of Barrow Village, no jaegers or owls were seen and no fresh sign of lemmings was found. On June 8, a few lemmings were caught in an area of large raised polygons southwest of the Base, and viscera of a few left by predators were found. On the same date three pairs of snowy owls and a few pomarine jaegers were observed. By the 10th, there was an increase in numbers of both jaegers and owls, but the jaegers were much fewer than in 1949. Two nests of the pomarine jaeger were found in 1950, one on our study area and one to the west of Dry Lake, but there is no record of an owl nesting near Barrow that season. Information summarized in this paragraph was provided by G. E. MacGinitie, R. Rausch, E. L. Schiller, and I. L. Wiggins.

In 1951, pomarine jaegers were present on June 6 when observations were begun. A few were seen by E. L. Schiller on June 3 in the course of a trip 30 mi. south of Barrow, but none near Barrow prior to the 6th. Until June 30, this species was present only in small numbers and was observed singly or in groups of 3 or 4. Once, on June 30, a group of 7 was observed. All were merely moving through the area; that is, there was no clear indication that any jaegers were locally settled even for a few days. After June 30, none was recorded except on August 7, when one was seen along the beach at Birnirk.

In 1952, snow persisted late; no pomarine jaegers were seen until June 9, although several observers were in the field daily from May 29. By June 12 the species was common generally over the tundra, and individuals resting on elevated, exposed patches of ground were seen frequently. In the following week jaegers became very common. Locally established breeding pairs defended their home areas against other jaegers which were moving through the area or wandering about in such numbers that much calling and chasing ensued, and the general confusion made

difficult any effort to distinguish between the then resident and the other, mobile part of the population. In the period June 12-22, numbers reaching 20 individuals per sq. mi. were present over much of the area near Barrow and the Navy Base, and in the light of the breeding density to which the population fell by early July, jaegers in the initial period of abundance were about five times as numerous as those comprising the stabilized breeding population. After June 22, numbers fell to a population which remained stable for five to six weeks, of four pairs per sq. mi. This figure is based on a total of 34 pairs located on a systematically surveyed area of nine sq. mi. (Fig. 3).

In the second week of August, numbers of jaegers seen along the ocean shore increased. On August 16, and for the first time since mid-June, jaegers present on the tundra between inlets opening into Elson Lagoon did not defend territories, and loose groups of undemonstrative individuals, of as many as 6 to 8, were seen frequently. Absence of young in this area, previously occupied by nesting pairs, indicated nesting losses may have in part been responsible for the local gatherings. After that date, previously resident birds began to desert home areas, territorial defense on other parts of the tundra gradually waned, and small flocks of 3 to 7 birds became more frequent.

After August 30, no territorial defense was observed and by the end of the first week of September, all areas where territories were previously held were deserted. In early September, both adults and young associated in loose groups, frequenting the ocean shore, the larger lakes, and ice floes. Jaegers seen 5 mi. offshore on ice floes on September 11 were chiefly adults, but one in a total of about 50 being immature.

In the latter part of the summer, no large groups were noted. Thus, on August 15, during a 12-mi. trip along the ocean beach southwest of Barrow, the total number of jaegers seen feeding among ice cakes and along the shore line was estimated at only 30-35, and records subsequent to that date refer to numbers less than 10 with no particular notice of aggregation.

In 1953, the first pomarine jaegers were seen on May 25, more than two weeks ahead of the earliest arrival in 1952. By May 28, a few pairs were already locally settled, and in the course of a survey over the tundra south of Barrow and the Navy Base on the 29th, numbers were estimated at 2-3 individuals per sq. mi. On June 1, a clear and exceptionally warm day, jaegers became abundant and conspicuously aggressive. Defense of territories was general from that date on. Estimation of densities in the first week was difficult, and it will suffice to say that numbers reaching several dozen per sq. mi. were commonplace. Subsequent survey of 7 sq. mi. over which breeding pairs were mapped yielded a total of 128 pairs (Fig. 4), or 18 pairs per sq. mi. Maximal densities reached 20-21 and 25-26 on two neighboring sq. mi., respectively, of more or less consistently suitable habitat; and the density on the northern half of a sq. mi.

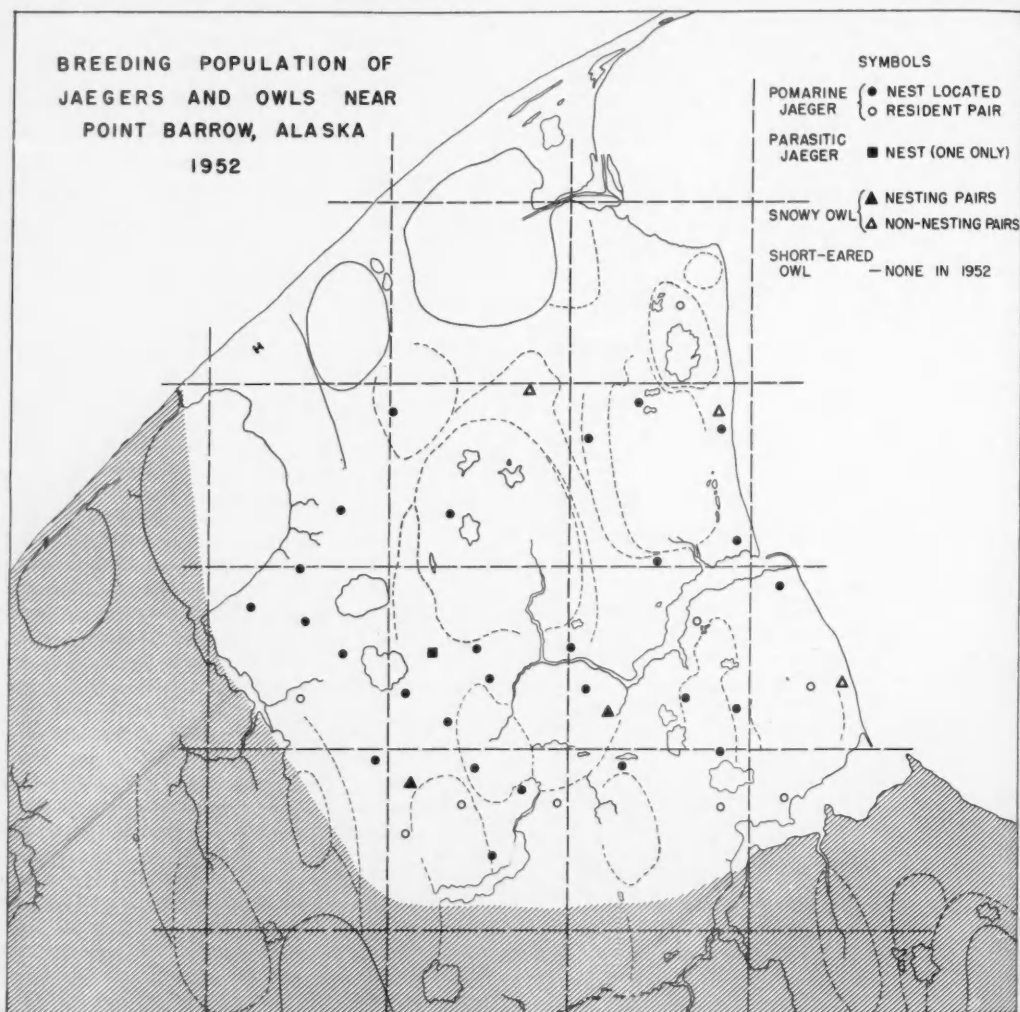


FIG. 3. Breeding populations of jaegers and owls near Point Barrow, Alaska, 1952. The overlaid grid indicates square miles. Shading incloses the census area. Broken lines indicate physiographically prominent breaks between marshy flats or old lake beds and neighboring, better drained ground.

along the southern margin of the survey area was such that it evidently supported about 25 pairs.

While a drop in numbers of jaegers took place through June, unlike 1952, wandering individuals occurred and provoked local territorial aggression almost without break through the summer. The presence of such birds is indicated additionally by the success of a few pairs in establishing territories in late June and early July near the ocean shore on tundra earlier ignored by jaegers; by the intermittent presence in early July of a well-marked dark-phase individual paired with a light-phase bird in one area which was defended but not occupied consistently and in which no nest was located; and by the short-term territorial residency of such pairs as are indi-

cated for the ridge plot in Fig. 6. Under such circumstances, any sort of estimate of the numbers of these birds would be difficult to make and no estimate was attempted. The facts stressed here are that there was a relative consistency in the occurrence of non-breeding birds and that these were either bona-fide non-breeders or birds locally displaced for one reason or another after attempting or starting nesting.

Flocking of non-breeding individuals or others no longer territorial occurred conspicuously and early, and gatherings of jaegers were recorded from late July on. By July 28 and in the following days, loose groups of 20 to 30, and one of 49, individuals were seen frequenting an area of a locally dense population of lemmings near the shore of Elson Lagoon, and

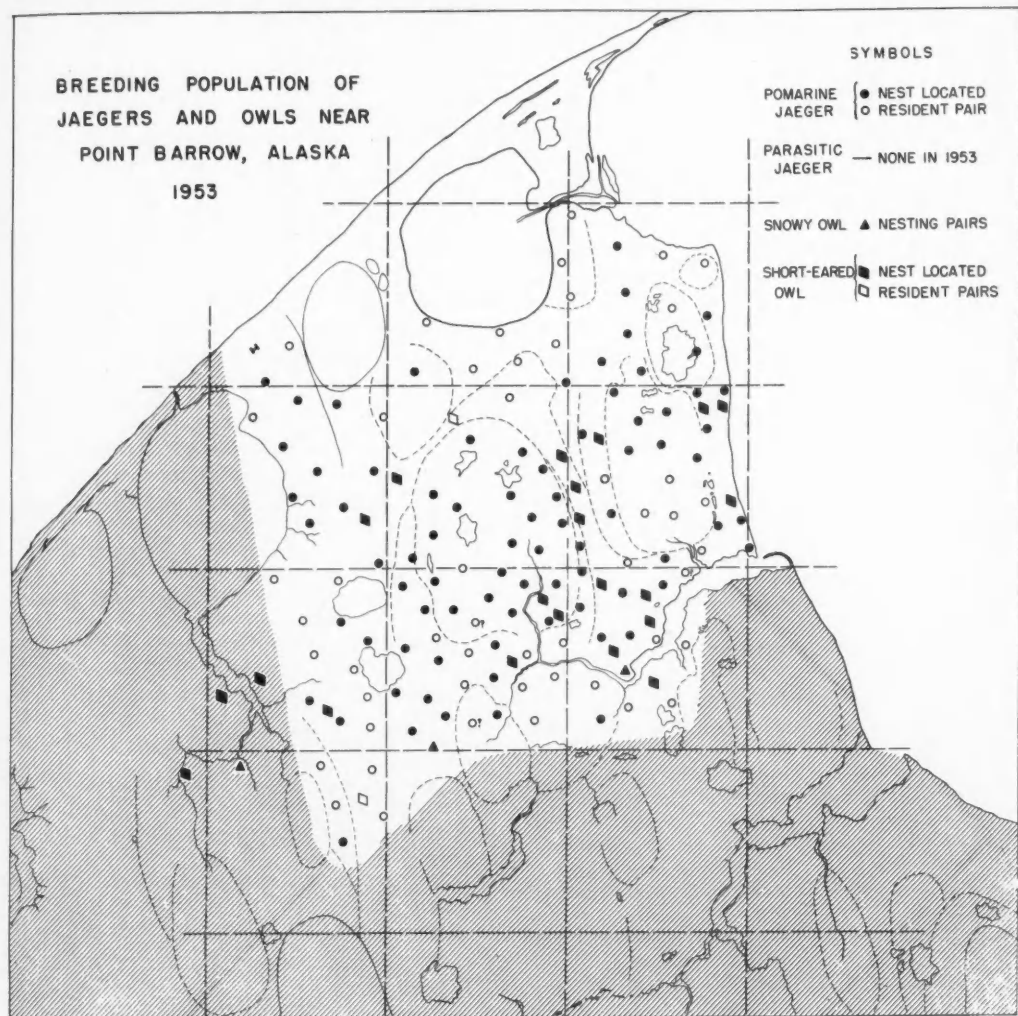


FIG. 4. Breeding populations of jaegers and owls near Point Barrow, Alaska, 1953. See Fig. 3 for explanation. No jaegers or owls bred here in 1951 or 1954.

in one case, such a group was observed flying westward over the tundra within a mile of the ocean shore. On high tundra, chiefly south of Barrow Village, where earlier in the summer jaegers and lemmings had been abundant, lemmings were scarce and jaegers absent on August 8. Such unsuccessful segments of the population would in part at least explain the increase in numbers of non-territorial birds tending to congregate, as noted in late July. In general, through August numbers of jaegers fell, although young and attending adults were seen locally as late as August 22. Observations stopped on August 24.

Thus, in 1953, the year of peak abundance in the lemming population, the jaeger population was not only more dense but also more fluid than in 1952.

In 1954, lemmings again became scarce and although jaegers were observed near Barrow from June 5 on, in the main they occurred singly or in small groups; no nesting occurred (M. E. Britton and W. H. Maher).

*Nesting cycle.* In 1951, no nesting occurred, and the species was relatively uncommon, as indicated by foregoing records.

In 1952, nesting began about June 20. First newly hatched young were found on July 17, and by the 20th, almost all nests contained young. Both sexes took care of the young, which were fed largely, if not exclusively, on morsels of meat torn from lemmings. Such pieces were regurgitated by some of the young handled during banding. As late as Sep-



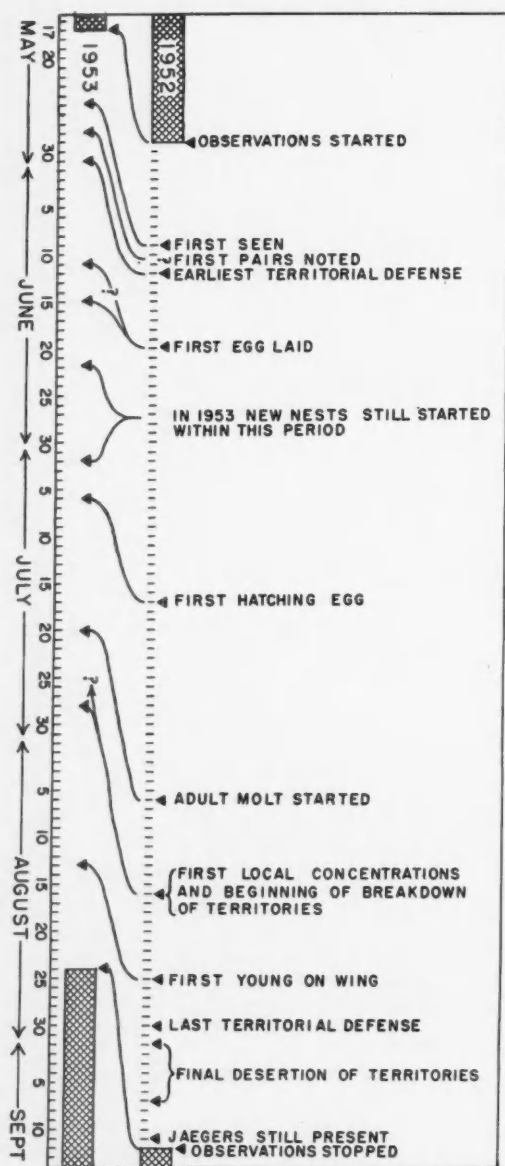


FIG. 5. Comparative chronologies of the breeding season of pomarine jaegers for 1952 and 1953.

tember 7, feeding of young by adults was observed, although by this time apparently all surviving young were able to forage by themselves.

In 1953, eggs were laid chiefly in the period June 16-19, although some were probably laid earlier, and some nestings were not started until the first week of July. Most young hatched in the period July 10-15.

On the basis of the observations of 1952 and 1953, the nesting cycle of the pomarine jaeger lasts 10 to

11 weeks. Incubation requires 27 or 28 days. Young do not fly until five to six weeks after hatching and they are attended by parents for at least a week more. Records in support of this chronology are summarized in Fig. 5. There it is shown that various events were first recorded 9 to 17 days earlier in 1953 than in 1952. It seems justified to say that for the population of breeding jaegers, the season of 1953 was 10 to 14 days ahead of that of 1952.

With respect to nesting success, the two seasons 1952 and 1953 clearly contrast. Hatching success, per unit of breeding effort or on a percent basis, was evidently lower in 1953 than in 1952. Unfortunately no quantitative data can be given in support of this point, but we do have considerable circumstantial evidence. In the sparse population of 1952, the relatively well synchronized nesting proceeded without incident, so to speak, once the pairs settled down to routines of incubation. We recorded no nest failures during incubation. All located nests contained two eggs, and hatching was successful in all those checked later except one. In this, the second egg produced a weak and somewhat deformed nestling which was gone a few days later. On subsequent visits to nests, for two weeks or so after hatching, both of two original young were typically present. After the exodus of non-nesting jaegers through late June, the population was stable and its members relatively settled in demeanor. In part these points are a matter of records, in part hindsight acquired as we recognized important differences between 1952 and 1953 through the latter season.

In the dense population of 1953, initiation of nesting on a population basis was not synchronized, indeed egg-laying occurred over a 20-day period. A number of nests contained only one egg when first discovered and on subsequent visits; these were found early enough that they were considered first efforts. In at least three cases, nests were destroyed in the egg stage, two of these representing the first and second efforts of one pair. Still other pairs located for variable periods on territories left them while neighboring pairs continued their nesting (Fig. 6). Some of these may not have actually started nesting, but it is unlikely that all left their territories without any egg-laying. In several nests, near or on census plots checked at hatching time, only one chick was present, the remaining egg disappearing after a few days. In one nest, one of two eggs was infertile. In the majority of nest areas visited after the chicks were one or two weeks old, only one was found on each. Finally, from an upland area of easily two sq. mi. where breeding pairs were generally distributed in June, jaegers were found gone on August 8, much too early for any young to have been raised successfully. Thus, we have no alternative but to conclude that nesting success, at least through hatching, was lower per unit of breeding effort in 1953 than in 1952. It is nonetheless possible that the total nesting effort over the 7 sq. mi. surveyed in both years may have produced a larger total number of young in 1953 than in 1952. This we do not know.



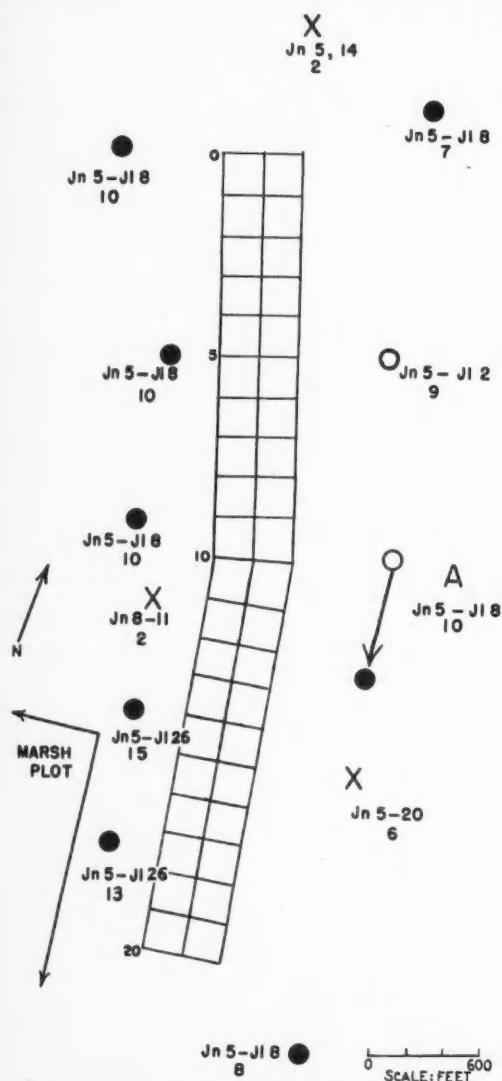


FIG. 6. Locations of settled pairs of pomarine jaegers near census plot 1 (20 x 2 acres) in 1953; with each record are given first and last dates of observation and below this the number of separate dates on which each pair was recorded; solid dots indicate nesting pairs with nests located; open circles indicate location of pairs whose nests were not found; X indicates pair present only in the early part of the breeding season.

In 1952, the nesting population consisted largely if not entirely of adult birds. These would be individuals two or more years old. Neither among specimens collected nor among those breeding were any noted to have the underdeveloped central rectrices seen among members of the 1953 population. In the latter year, therefore, a small percentage of the breeding population consisted of individuals with sub-adult plumage characters, and these were proba-

bly no more than one year old. Some of these were collected, including one female which had laid a clutch of two eggs and another which had laid one egg and was shortly to ovulate a second. Dark-phase birds were more numerous in 1953 than in 1952; data on their occurrence will be presented elsewhere.

*Territoriality.* The foregoing sections on abundance and nesting have already brought out several facts concerning territoriality in the pomarine jaeger. Jaegers arriving on breeding grounds become territorial any time from the last week of May through the first two weeks of June (or even later, in a minor part of the population, as in 1953). Territorial behavior begins one to two weeks before eggs are laid. Members of a breeding pair defend their areas by calling and chasing and are persistently alert for intrusions of both resident neighbors and local vagrants. In a breeding population, and particularly in the dense one of 1953, the pattern of territories is diagrammatic, as Manniche (1910) also remarks for the long-tailed jaeger. The pairs are spaced out with remarkable regularity (Fig. 7), and the nest is generally placed in the approximate center of the defended area. Territoriality continues through the period that young are dependent and begins to wane (at least in 1952) in the last two weeks of August. Breeding pairs normally confine their foraging to the territory.

In the essential features of its territoriality, the pomarine jaeger resembles many passerines, but lacks

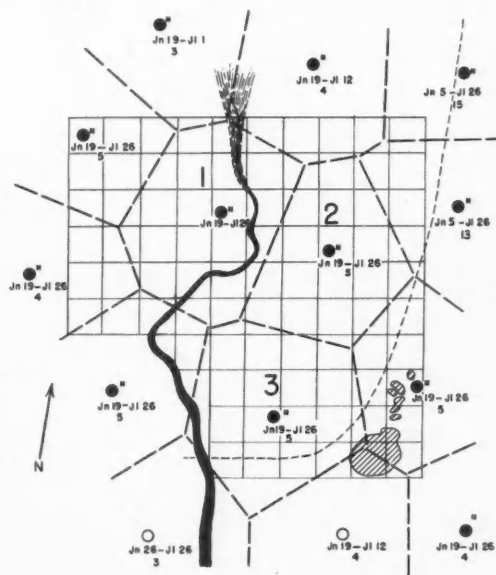


FIG. 7. Territories of pomarine jaegers on plot 3 (flat marsh) in 1953, showing periods and numbers of records as in Fig. 5; the 86-acre plot (grid of acres shown) was crossed by a stream channel and included several small ponds in its southeast corner; lines indicating approximate boundaries of territories are equidistant between neighboring nests (solid dots) or activity centers (open circles).

song (or at any rate a regularly delivered vocal announcement). On the basis of Armstrong's (1947) classification of territories, that of the pomarine jaeger subserves functions of both reproduction and self-preservation.

Territorial actions, displays, and other features of breeding behavior are described elsewhere (Pitelka *et al.* 1955). Here the remaining consideration of sion and territory size. For two plots, the periods of recorded occurrence and the number of days of record are given in Figs. 6 and 7, and from these it is evident that the occurrence of resident pairs at "home-sites" was consistent. The fact is that the data given in the figures are summaries of records formally entered in notebooks and on census sheets, and most of the pairs were noted in the field many times more when other work was underway.

In plot 1, in 1952, four pairs, usually present some distance away from the ridge on which this plot was located, would forage near it, two pairs on each side. Territorial strife between two pairs, oriented along the ridge as a boundary, was watched on June 26, and by their flight paths on other occasions, also, the settled pairs showed that the ridge was recognized as a boundary. In 1953, there were nine pairs located along and close to the plot (Fig. 6) with others not far beyond. Again, the ridge was used consistently as a boundary by pairs located on the two sides.

Nowhere in the entire area surveyed in 1953 were jaegers as dense as they were along the east side of Central Marsh, particularly at its east margin, along the west side of plot 1. This must surely be close to maximal density for a large territorial predator such as the pomarine jaeger.

On plot 2, in 1952, two breeding pairs occurred, one located to the north, the other to the south. In 1953, although no nests were located on the 20 ac. rectangular area, four pairs (and possibly five in late June) were located close to it, with three of these regularly cruising over portions of the plot included in their territories.

On plot 3, in 1952, but one pair regularly occupied or at least hunted over only the southern part of this marsh area, the nest being located to the south of the plot and east of the stream draining it (Fig. 7). On June 26 and 29, 4 to 6 additional individuals were present briefly, but it was not until July 17 that an additional jaeger was observed. On that date a jaeger apparently belonging to a pair located to the north flew across the marsh from the east, then turned south, and when halfway across the plot, it was chased back to the north by a member of the resident pair. Such incidents were relatively infrequent in the widely dispersed breeding pairs of the 1952 population.

In 1953, jaegers were more numerous on plot 3, and the smaller territories led to much local strife with frequent boundary conflicts among neighbors. The distribution of breeding pairs is shown in Fig. 7. Location of nests are precise for the plot itself, approximate for the area around the plot. Whereas in

1952, the number of pairs using the marsh plot was but one or possibly two, in 1953 the territories of three pairs were confined to it and those of 10 or 11 pairs along the periphery of the plot lapped over more or less onto it. The nests of two of these pairs were also placed on the census plot. These pairs were almost as closely spaced as those on the west side of plot 1.

Over a disturbed area of about 50 ac. behind the Arctic Research Laboratory, in 1952, resident jaegers did not occur regularly until early August, when one pair located inland enlarged its hunting range to include the area. In 1953, four resident pairs made use of the same area, and the territories of two of them were largely confined to it.

Thus, from 1952 to 1953, densities of breeding jaegers increased locally 2 to 6 times, and the overall increase was  $4\frac{1}{2}$  times the 1952 density.

From data obtained on the large-sized plot 3, it is possible to provide an estimate of minimal territory size inasmuch as three territories were wholly contained within this 86 ac. plot. The nest is typically more or less in the center of a territory, as we ascertained many times by watching, under duress as it were, the aggression of neighboring pairs as we moved across successive territories. It is therefore reasonable, for purposes of the desired estimate, to divide the distance between nests of neighbors and thereby to delimit their respective territories (Fig. 7). Because of neutral zones between territories (Pitelka *et al.* 1955), it would hardly be justified, without prolonged observations and systematic tabulation of contact incidents between neighbors, to set forth a precise measurement of the areas of these territories. But it is significant for us to know what the order of the figure for minimal territory size is. As Figure 7 shows, for so large a predator as the pomarine jaeger (600 to 900 gm.), it can be so little as 15-20 ac.

The matter of territory size can be examined further by use of distances between mapped pairs. Using data given for the marsh plot in Fig. 7, we can measure distances between pairs 1, 2, and 3, those from each of these pairs to all its other neighbors, and those between pairs along the periphery. The result is 28 separate measurements, taken to the nearest 100 ft., for approximate distances between centers of territories. Eighteen such measures may be obtained from data occupying marsh and low tundra along two sides of plot 1, as shown in Fig. 6. Temporary presence of three additional pairs is also shown in Fig. 6, but these did not enter into the series of 18 measurements. Finally, three measures are obtained between four pairs nesting along the axis of and close to plot 2.

A percent frequency distribution of the inter-pair distances is given in Fig. 8. Because of the special attention given to these three plots and their surrounding areas, they provide the best data on spacing of breeding pairs in the 1953 population. The distances are small enough (over 62% below 1200 ft.) that enlarging the sample from less intensively studied

areas is not safe. For 1952, however, it is necessary to take a sample of the less precisely spotted pairs, and this has been done using the 2 sq. mi. along the southern border of the survey area (Fig. 3) where breeding jaegers were densest. Distances were taken between pairs of these unit areas and also between the peripheral ones and their closest neighbors on adjacent square miles. These were determined to the nearest 100 ft., but only to make the intervals between frequency classes in the two years comparable.

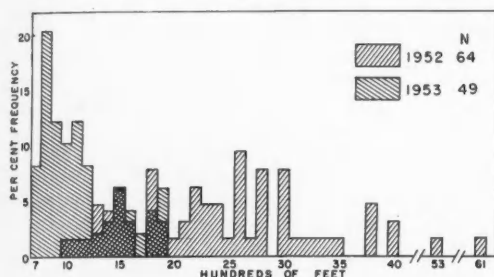


FIG. 8. Percent frequency distribution of distances between nests or activity centers of territorial pomarine jaegers in 1952 and 1953; the number of records for each year is given beside the legend above. See text for further explanation.

Actually, the error in the 1952 mapping is not  $\pm 50$  ft., as the measures imply, but  $\pm 100$  or 200 ft. The reader is reminded of the exceptionally advantageous circumstances we enjoyed in carrying out the original mapping. We consider the estimate of error a safe one. The larger error of the 1952 figures needs to be recognized, but the validity of ultimate extrapolations is not influenced by the fact of this larger error.

For 1952, 64 measures of distances were obtained between pairs of a group as delimited above, and the percent frequency distribution of these is also given in Fig. 8. There is a modal group in the section 2100-3000 ft., with 47% of the measures falling here. Thus a rounded figure of 1000 ft. is indicated for 1953, whereas 2500 is indicated for 1952. We venture estimates of territory size using the rounded figures for distances between pairs as their diameters. The polygonal form of the territories in continually occupied habitat permits this. For 1953, this is 18 ac., which agrees with direct determinations for three territories on plot 3. For 1952, this figure is 110 ac. This applies to the area where the jaegers were densest and the figure is therefore an approximation of minimal territory size under circumstances of food availability prevailing in 1952. The figure appears reasonable because 110 is about six times 18 (both figures represent areas with near-maximal densities), and the over-all density of 1953 was four to five times that of 1952.

The figures are of interest of themselves in revealing a magnitude of variation in population density in a predator species associated with a lemming cycle. In addition they can be used in calculations

of food consumption with relation to prevailing lemming numbers. Perry (1949) reports that average distances between territorial mounds and nearby nests of the great skua and parasitic jaeger on the Shetlands were 58 and 77 yd., respectively. For the latter species Dementiev *et al.* (1951) report distances of 50 to 100 m. between nests. These distances are considerably below the minimum interval (700 ft.) for breeding pairs in the dense population of pomarine jaegers in 1953, and the difference reflects a basic divergence within the genus *Stercorarius* (*sensu lato*) in organization of breeding populations, to be noted below.

Although the territorial behavior of jaegers has been noted by previous observers (Manniche 1910, Salomonsen 1951, and others), the statement of this observation is rarely supported by details, and in any event refers to the two smaller species, *parasiticus* and *longicaudus*. Only Schaaning (1907) declares breeding pairs of *pomarinus* to be territorial, but his observations have apparently been overlooked. In his accounts of *pomarinus* and *parasiticus*, Salomonsen (1951) refers to nesting "colonies" at the same time that, under *parasiticus*, he acknowledges the territoriality of that species. There is nothing colonial (which implies social organization of breeding units) about *pomarinus*, as Schaaning (1907) and Zhitkov (1912) long ago pointed out, and this statement apparently also applies to *longicaudus* (Manniche *loc. cit.*; Løppenthin 1943). The word colonial is misused in other parts of the literature on birds when a breeding group, territorial *inter se*, is delimited because only an island of habitat is available. This is no basis for use of the word colonial. Also, the fact that there may be consequences related to initial population size does not justify use of the word colonial. If the pomarine jaeger is colonial, then so is every territorial species, for the simple reason that recognizable groupings of individuals naturally occur wherever there are recognizable isolates of its habitats. The great skua (*Stercorarius skua*) is said by Witherby *et al.* (1941) also to nest in "colonies," and Witherby indicates further that nestings are not close together. In the skua foraging ranges are at varying distance from the nesting area and apparently not mutually exclusive among breeding pairs (Perry 1949). Thus, there appears to be a fundamental difference in population organization between the skua and at least two species of jaegers.

One pair of parasitic jaegers watched by us was territorial, and comments of Salomonsen (1951) suggest that at least away from the coast, this species is territorial. Bertram & Laek (1933) likewise suggest living areas for *parasiticus* which may have been self-contained, as they say pairs were isolated and kept to their particular areas throughout the summer. But from the description given by Perry (1949) of breeding distribution on the Shetlands, the breeding organization of *parasiticus* is here not perfectly territorial but more like that of the large skua (Gibson-Hill 1947, and Dementiev *et al.* 1951). Nicholson

(1930) states specifically that in Greenland he found *parasiticus* not strictly territorial. A variation in breeding organization of the type which the available evidence suggests for *parasiticus* apparently occurs in the glaucous gull, some breeding populations of which are truly colonial, while others consist of scattered solitary pairs (Salomonsen 1951).

This entire matter, whether or not these birds are colonial, or basically what differences may exist among them in population organization, should receive more attention from future observers in the arctic. It is conceivable that any species of jaeger, although breeding, may not be relying upon such a local food source as lemmings which, so to speak, allow out-and-out territoriality. If alternative forms of population organization can occur, this variation would be of great theoretical interest. The parasitic jaeger evidently exemplifies such variation. These comments are prompted not only by study of the literature, but also by our observations of *pomarinus* in the latter part of the 1952 season. At this time there was a tendency for at least those pairs near the ocean to forage along its shore and thereby to enlarge their territories. Such enlargement presumably could permit overlap of foraging ranges. While attention is called here to circumstances which could lead to a breakdown of territoriality, as far as our observations of *pomarinus* go, for pairs attached to areas with nesting underway, hunting ranges were or tended always to be mutually exclusive.

**Predation and hunting behavior.** Jaegers normally stand or sit on some slight prominence, using even the gentlest rise of a few inches in particularly flat areas. From such a resting site, in the first half of June when there is a patchwork of exposed ground and snow and when lemmings are frequently seen moving against the white background, a jaeger flies out directly to a lemming, seizes it with its bill and usually flies back to the favored mound before consuming any of it. Under such circumstances, jaegers sight and fly directly to lemmings at distances of at least 500 ft. In flight, if a jaeger with quarry is under attack by others, the food may be bolted on wing. We have witnessed this and have also opened one or two stomachs with virtually intact but moderate-sized lemmings. Usually, however, the lemming is torn and eaten in pieces. This was true in 1953 when food was abundant locally, but may be less true of seasons when the food supply required by a breeding pair must be sought over a larger area. Thus, in 1953, many finds of torn or partly eaten carcasses of lemmings in areas where jaegers were breeding indicated an abundance of food, whereas in 1952, such waste was not seen.

Hunting occurs both on wing and on foot. On the wing, the jaeger, may "tred" air in the manner of a sparrow hawk, but this is relatively infrequent. Generally hunting occurs in the course of a cruising flight over the territory, the jaeger watching the ground below with bill pointing down. When a lemming is sighted, the bird comes down directly to seize it or

to dig and tear at the shallow and usually loose burrows and tunnels. Occasional observations of jaegers tussling with lemmings and failing to retain hold indicate that at least large-sized individuals, which in Lemmus reach 100 to 125 gms., may be difficult to manage. Much of the hunting on foot occurs at burrow systems, such as those through soft moist vegetation on ridges of low-center polygons. Here the jaeger tears the burrow roof, throwing bits of vegetation aside. This manner of hunting occurs both early in the summer when the jaeger may work at the margin of a snow patch riddled by tunnels or later when the tunnels are under vegetation. Groups hunt similarly. On July 29, 1953, 24 jaegers were flushed from near Brant Point where, over an area 50 ft. wide, they had opened and worked over thoroughly a runway system, so that sod tufts picked from the runway roofs lay scattered everywhere. We have never witnessed a successful act of predation when a jaeger hunted in this manner, and the behavior, though persistent, seemed at times casual and aimless, particularly since the burrow systems are usually networks of tunnels providing several avenues of escape for the lemming. It is true, however, that if not successful in grasping an occasional subadult or adult by this method, the jaeger could locate nests and young (Birulya 1905). At any rate, Pomarine Jaegers every now and then indulge in a deliberate and more or less methodical ripping of surface tunnels, and it is safe to assume that this effort must be rewarding if the pattern of behavior is so clear.

Jaegers are known to prey on birds such as phalaropes and sandpipers, which they can catch on wing (Tuttle 1911; van Oordt 1921; Congreve & Freme 1930). On August 20, 1952, one of us witnessed three jaegers on wing pursuing red phalaropes moving along the coast in large flocks. One jaeger would seize the wing of a phalarope with its bill, toss the bird about, then release it. No actual kill was witnessed in the course of a half hour's observation, but in this time six phalaropes were struck. Thus, the behavior appeared to be only a playful tormenting of the phalaropes, but by such actions jaegers can become effective predators, as the reports cited above indicate. Otherwise, in the three years, we did not witness directly any predation by pomarine jaegers upon small birds, but they were suspected to be responsible for some nest losses of lapland longspurs, ducks, and shorebirds. At three destroyed nests of the short-eared owl, beak marks in the eggs pointed clearly to the pomarine jaegers, and circumstances at a fourth also implicated the jaeger.

No out-and-out parasitism was observed among territorially settled pairs of jaegers, and there was little indication of this among members of groups. Brief frays, as occur typically among gulls, occurred among jaegers when one picked up a piece of food. We did not witness adult jaegers pursuing gulls and prompting them to disgorge food, certainly not as a matter of habit. This manner of food gathering could support very few jaegers indeed in the Barrow area.



But on August 30, 1953, young of the year were observed pursuing glaucous gulls and picking up disgorged food. Salomonsen (1951) also reports chasing by newly fledged young, in this case other pomarine jaegers. That parasitism might occur was suggested on June 15, 1951, when members of a loose flock of arctic terns moving across the tundra near Elson Lagoon mobbed and chased two pomarine jaegers which left the area without defense. The terns may have belonged to a nesting colony on Deadman Island, one of several gravel bars inclosing Elson Lagoon along the north.

The other two species of jaegers were noted feeding on birds' eggs, insects, and plants, as they are known to do in other parts of the arctic. The nesting pair of parasitic jaegers in 1952 was preying on lemmings, and apparently this was its primary food, but on July 17, both birds landed at the nest of a red-throated loon about 300 ft. away from their own nest and destroyed both eggs, eating some of the contents at the nest and then carrying one away. The loon was frightened away by men examining the jaeger nest, and the jaegers went to the loon nest during this interval.

Stomach contents of three long-tailed jaegers collected on July 3, 1951, near plot 2 included a considerable quantity of matted, coarse fresh-water alga (like *Vaucheria*), insects, and the crushed, slightly discolored shell of a shorebird's egg, which appeared to be that of the red phalarope, a species that was nesting commonly in the area. The insect remains (identified by Dr. Paul D. Hurd) included the following:

NAME	Numbers of Individuals in 3 stomachs		
Diptera			
<i>Tipula carinifrons</i> Holmgren	3	0	1
Coleoptera			
Dytiscid sp.	6*	1	3
Carabid sp.	0	5	2
<i>Chrysomela subsulcata</i> Mannerheim	0	1	3

\* One a larva; all other insects listed were adults.

Of two stomachs from the same species collected at East Oumalik, in the Brooks Range foothills, on July 17, 1951, one contained a few blades of grass and the other contained egg-shell fragments. The stomach of a female long-tail collected at Barrow on July 8, 1949, by R. Rausch contained one brown lemming.

**Field Use of Plumage Characters.** For all our observations of the breeding pomarine jaegers, but particularly for those on territoriality, the variation in plumage, among individuals of a large species living in open country, was a most happy circumstance. In addition to the well-known light- and dark-phases, the light-phase individuals vary among themselves in amount of darkening of the venter, and indeed some of the darkest are regarded as "intermediates" between the two phases, as noted by Southern (1944) and Murphy (1936). There is a quantitative color dimorphism between sexes, however, not noted by Southern. The males are whiter ventrally and darker on the

lower belly and crissum (usually solidly dark grey in adults). Superimposed on such variability is that of age, with younger individuals showing more ventral barring and less even dorsal coloration than older ones. Also, there is a recognizable difference in the size and position of the central rectrices between sub-adult and adult birds (Salomonsen 1951).

Examination of the series of specimens in several collections leaves us uncertain whether a clear-cut separation of the two age-groups can be made on the basis of rectrices. In adults, those of the smaller sex (males) are actually longer, on the average, than those of the larger females, which therefore as a group tend to be more or less intermediate between the adult males and the considerably variable younger birds. Nonetheless, a definite proportion of the sub-adult birds, and perhaps one significant enough to be usable in the field, have center rectrices which are not only shorter but have only a partial twist terminally, or none at all. This feature also can help the field observer to distinguish at least some members of locally settled pairs. We were able, therefore, in the course of repeated observation of locally settled pairs, to use the characters just enumerated and so to become acquainted with many pairs. Thereby, at least some of any significant local changes could be detected, if any occurred, and a picture of spatial relations could be better developed. The rule was that breeding pairs remained locally put.

Our field acquaintance with plumage variation in this species together with study of specimens obtained by us in the field and also those in several collections lead us to suggest that the sequence of plumages described by Bent (1921) and Witherby *et al.* (1941) is in need of critical review particularly because of the bearing of this matter on further study of the population ecology of jaegers. According to the authors cited, a pomarine jaeger does not assume its fully adult plumage until after the third summer, or in the course of its fourth year. We venture to suggest that there may simply be two groups after the first autumn, one consisting of adults and the other consisting of highly variable first-year birds which undergo a highly variable postjuvinal molt. The plumage cycle would then resemble that of smaller gulls like *Larus ridibundus* and *L. philadelphia* (Dwight 1925). In association with this variation of the first-year birds is their scattered distribution in the first year, some individuals remaining on wintering grounds, some moving northward, others reaching the breeding grounds and perhaps even breeding. The models for this simpler picture of age-groups would be arctic shore-birds such as *Limnodromus* (Pitelka 1950) and *Phalaropus* (Pitelka MS), which are known to display in their first year a variable plumage and a variable degree of movement back toward the breeding grounds. Moreover, a three-year plumage cycle, if the situation in gulls has a bearing here, implies little or no breeding in the first and second years of the life-span. Since the pomarine jaeger is a lemming predator, terrestrial and non-colonial in its breeding distribution, and one whose populations



experience years when breeding may not occur, it seems to us asking rather too much that this species face regularly the risks implicit in a life-cycle with recurring years of non-breeding when already there are serious uncertainties, so to speak, presented by the food source which sustains its breeding. Available descriptions of plumages do not take into account the sexual dimorphism mentioned above, and this suggests that perhaps earlier students were misled by the considerable plumage variation and were inclined to assume that jaegers are comparable in their plumage cycles to the larger gulls.

If the sub-adult birds of the 1953 population are not first-year birds, and if in fact they were two or three years old, then there is presumably a group of first-year birds none or few of which showed up on the breeding grounds—a group whose characteristics should show up as a modality in the array of variation observable in a good series of museum skins. The existence of this modality has been proven by no one. Wynne-Edwards (1939) has suggested that pomarine jaegers in their first year may remain on the oceanic, low-latitude wintering grounds. Earlier (1935), he had noted that summer records for *pomarinus* from mid-latitudes “must be exceedingly scarce,” a detail which was used in support of the aforementioned suggestion; but such mid-latitude occurrences must be more or less irregular, even when accumulated along any given sector of coast line. That *pomarinus* can occur in mid-latitudes in summer is indicated by Grinnell & Miller (1944) for the California coast.

This brief review suffices to emphasize the basic importance of further study of the plumage cycles of jaegers. Whatever its outcome, in this paper, only two recognizable age-groups are considered to have been represented among the breeding pomarine jaegers.

## 2. SNOWY OWL

In northern Alaska, the snowy owl is a resident species, its numbers varying according to the abundance of lemmings there as elsewhere in the arctic. It may remain near Barrow through the winter when lemmings are common (Bailey 1948), and it is in fact known to winter at even higher latitudes (Maniche 1910; Pleske 1928).

The literature for the snowy owl is far more extensive than that for the pomarine jaeger, and what information we gathered agrees closely with reports of earlier observers (particularly Pleske 1928; Murie 1929; Sutton 1932; Bent 1938; and Salomonsen 1951). This account, therefore, confines itself more to the Barrow scene and deals mainly with our observations on numbers, nesting, and predation recorded at nests. Data on predation from extensive collections of pellets will be reported upon later.

*Relative numbers.* Available information about occurrence of snowy owls near Barrow in 1949 and 1950 has been summarized with that for the pomarine jaeger under the latter species. In general owls were present in small numbers, at least in May and June, in both of those years. Owls were also present

through the winter of 1948-49. A nest with five young was found on July 22, 1949, near Cape Simpson (about 50 mi. ESE of Barrow); but there is no 1949 record of a nesting closer to Barrow, and none was recorded in 1950 (G. E. MacGinitie and R. Rausch, *in litt.*).

In 1951, snowy owls were present in small numbers near Barrow through most of the summer, but we found no evidence of nesting. One owl was seen on June 7 when observations were begun, and the species was reported to be present earlier, on May 31 when two seen on the ocean ice were thought to be feeding on eiders. In view of the fact that lemmings were scarce through the winter of 1950-51, it is doubtful if owls were present locally prior to the appearance of migrating birds. After June 7, but one owl was seen on each occasion of a record through June 17. An emaciated adult male found in the snow on June 11 apparently had starved recently (weight 1185 gms; testes small, 8 mm long). None was then seen near Barrow for over a month, although one was sighted from a plane south of Admiralty Bay on July 11.

From July 21 to August 16, 1 to 4 owls were seen on trips up to 3 mi. away from the Base. As many as four were present on August 10 on an area of about 2 sq. mi. where sandpipers and longspurs were common. In fact, the availability of small birds in the latter part of the season was probably the chief factor responsible for the slight rise in numbers of owls recorded. Owls were not recorded again by us after August 16.

Neither snowy owls nor any pellet signs were recorded at East Oumalik in the period August 1-7, although at that time microtine rodents (*Microtus oeconomus* and *M. miurus*) were fairly common.

In 1952, owls were more common than in 1951 and they also bred locally. They were present at least by May 25, when 5 or 6 were seen by Robert Rausch over the 12 mi. distance between Barrow Village and the Monument to the southwest. After that date owls were seen regularly until September 8, the last date of field work on the tundra south of the Base.

From late May until late June, owls increased in numbers. In late June and early July, maximal densities were estimated at 5 per sq. mi., including both breeding and non-breeding individuals. This estimate is based on an area of about 9 sq. mi. over which a survey of lemming predators was conducted (Fig. 3). On clear evenings when visibility was good, 10-15 owls could be sighted with 8x binoculars over the extensive marsh flat, through 180 degrees along the horizon, between high tundra about 2 mi. south of the Base and Elson Lagoon to the east. These owls would be scattered over an area of about 4 to 5 sq. mi. From early July until late August, numbers fell off steadily, and a marked drop occurred in late August and early September. On three trips south and southeast of the Laboratory between August 25 and September 5, only one or two owls were sighted per mile of travel.

Three nests were located near Barrow in 1952. Two are shown in Fig. 3 along with three pairs of

owls settled locally and observed repeatedly at or near the spots marked on the map. Some owls other than the three pairs whose nests were found of course might have at least started nesting in late May or early June, but even allowing for these possibilities, most owls seen in the period when lemmings were abundant, after the melt-off of snow in the latter half of June, were wandering locally. Hence it is safe to say that less than 50% of the peak population nested or even began nesting. In that part of the population of 1952 which stayed put over the survey area, distances between pairs were 1-2 mi., and areas of 2-4 sq. mi. evidently sufficed as territories. This estimate is supported by Shelford's (1943) report of a nest every two miles of a sandy ridge near Churchill, Manitoba, in 1933, a lemming year. No other reports of Snowy Owl breeding densities have been found in the literature.

In 1953, owls were present when observations began on May 17 and were seen throughout the summer. The last recorded observation was August 15, but owls were no doubt present after that date. Field work ended on August 24.

Prior to the melt-off of snow, which began in early June, and from May 20 to June 4, one to five were seen on various trips on the tundra up to two miles' distance from the Base. Nesting was underway in the first week of June. Local concentrations were first witnessed on June 7 when 10 to 12 were present at Nuwuk and on the ocean ice, gravel bars and beaches, and marsh flat nearby. On the 14th, 18 were present on an area of about  $\frac{1}{2}$  sq. mi. east and south of the so-called "drum area," a rectangular strip behind the Arctic Research Laboratory littered with empty oil drums, some of them stacked. These formed windbreaks used for shelter by the owls. Later the same date, 14 were counted over the same area. At Nuwuk, on the 15th, 24 were counted, and 7 or 8 more were seen along the 5 mi. oceanside route to Nuwuk. On the 24th, along the shore of Elson Lagoon, north of the mouth of Wohlshlag Slough, nine were counted. In the same period, June 7 to 24, one to five were seen on various occasions at localities up to 10 mi. inland. The sites of most of these concentrations, in June of 1953, were marginal areas where owls could avoid the jaegers common over the tundra, and unlike 1952, non-breeding owls did not occur scattered over the tundra.

After June 24, numbers fell off but owls remained relatively common to mid-August, when observations stopped. Until then, 1 to 7 were recorded on various trips on the tundra for distances of one to two miles inland. From early July on, these small numbers included non-nesting owls occurring irregularly and scatteredly over certain sectors of the tundra near the shore whereas in June such occurrences were few.

Three nests were located near the Base, on June 1, 22, and 26 (Fig. 4), with clutches of 6, 9, and 6, respectively. Four more were located on June 16 near Barrow-3, 10 mi. south of Barrow Village, with clutches of 8, 7, 7, and 4. These four nests were not visited again, but the first three were followed.

From nesting densities near Barrow in 1952 and 1953, it seems reasonable to estimate that the smallest territories of these owls are of the order of 2 sq. mi. This estimate is based on the distribution of pairs in 1952 and 1953 in the survey areas shown in Figs. 3 and 4, on the location of additional pairs southwest of these areas, and on the location of four neighboring nests found inland near Barrow-3 on June 16, 1953, along a route followed more or less eastward from Barrow-3 and then retraced westward. These nests were  $\frac{1}{2}$ -1 mi. apart.

Near Barrow, there was no significant difference in the numbers of nesting owls between 1952 and 1953. With a species whose breeding pairs are so widely spaced as in the snowy owl, it is likely that the area we examined was much too small to provide an adequate indication of any difference between the two years. Still, in view of the evidence from pomarine jaegers and short-eared owls, one would expect some sort of signs in 1953 in the snowy owl population, even in the area studied, reflecting the greater abundance of food that year. A difference in actual numbers did occur; in 1953 owls were more numerous and the proportion of non-breeders was higher. These non-breeders were present in largest numbers in June, and they did not occur dispersed over the tundra, as was the tendency on 1952, but rather in local concentrations already discussed above. Again it is suggested that the large numbers of breeding jaegers were a factor influencing the behavior of the owl population.

In 1954, scattered individuals occurred in the Barrow area from the first week of June at least until mid-July, and no nesting took place (M. E. Britton and W. H. Maher, *in litt.*).

*Nesting cycle.* The complete nesting cycle occupies over three months, probably  $3\frac{1}{2}$  months, although there appear to be no satisfactory records for the latter stages of nesting. What information we have gathered on the nesting cycle at Barrow fits in with that provided by Murie (1929), Sutton (1932) and the compilation of Witherby *et al.* (1940). Data on clutch size in lemming years are given in Table 1. Nesting records from Barrow will now be summarized.

#### 1952

*Nest 1.* When found on June 7, this nest contained only one egg. At the edge of the nest was an intact, full grown female *Dicrostonyx torquatus* (96 gms). When approached, the female flew down a gentle slope and, alighting on a snow bank, performed a pre-copulatory display. The male came directly and copulation occurred. Subsequent efforts to relocate this nest were unsuccessful, although the pair was still present in the area on June 12.

*Nest 2.* This nest was found on June 30 by Groth. The completed clutch was six. On July 20 this nest contained four young only, and it was later found destroyed, by means unknown, before any young left.

*Nest 3.* When found on July 14 by Treichel, this nest contained 3 eggs and 1 young 3-4 days old. Hatching of the second egg was already started

TABLE 1. Clutch-size in the snowy owl in lemming years.

Size of set	FREQUENCIES		
	Novaya Zemlya 1903*	Hooper Bay 1924**	Barrow 1953†
4.....	0	0	1
5.....	1	4	0
6.....	9	4	2
7.....	9	4	2
8.....	1	5	1
9.....	2	3	1
10.....	0	3	0
11.....	0	1	0
Sample size.....	18	24	7
Average clutch-size.	6.9	7.5	6.7

\*Only nests observed with completed clutches started prior to June 15 are listed here; these are the first 18 nests listed by Schaaning (1907:50) and retabulated by Pleske (1928:169).

\*\*Only nests observed with completed clutches in late May or June are listed here, from a series of 38 nests found in the area between Hooper and Igiak bays, Alaska (O. J. Murie, letter, January 16, 1954).

†Two nests in 1952 contained 4 and 6 eggs, respectively.

when the nest was visited on the 15th, and on the 17th it contained two eggs and two young. On July 20 there were 3 young and the remaining egg was pipped. On the 23rd, there were four young. In this nest, then, hatching of the four eggs was spread over at least a week and probably over a 10-day period. On August 6 the nest was empty and only one young was located about 30 feet away. Apparently this same juvenile, now able to fly, was found near nest 3 on September 8, and it was the only one successfully reared.

On July 28, the four young were weighed. At this time the estimated age-range was 7 to 17 days. The weights were 77, 159, 272, and 545 gms. In the previous 48 hrs., both sexes, but chiefly the male, brought food to the nest, but there was some indication that the pair might not be obtaining enough food. Thus, the female called regularly and this calling increased in frequency when the male was nearby with food; apparently the call was used as a food-need signal. The female herself left the nest a number of times to forage, and from most of these trips she returned unsuccessful. In the 48 hr. period, the female fed the young only seven times. Six feedings lasted 2 to 20 min., but one was spread over 34 min. The largest young was over seven times the weight of the smallest, and this variation in weights is considerable by comparison with the variation in a larger, but well-fed brood from which data were obtained in 1953. This seems to be a valid point notwithstanding the possibility that in the small '52 brood, ages of the four young might have varied more than those of any consecutive four in the '53 brood. This latter circumstance, if true, would also point to a more limited food supply in the area supporting nest 3.

#### 1953

*Nest 1.* Five of the six eggs found on June 1 disappeared in the period June 10-15, but the female

remained at the nest. From the remaining egg, the nestling was raised successfully and was seen away from the nest on several dates in July. When last observed, on July 16, it was 200 ft. from the nest mound and among high polygons where it would find relatively good shelter.

*Nest 2.* Eight of the nine eggs at this nest hatched, and the success of this nest was almost spectacular, with the young progressing satisfactorily until July 21 when men from the Base killed the female and brought five of the young into one of the repair shops. Up to then the indications were that most of the young would be raised successfully.

When this nest was discovered on June 26, five eggs were already hatched, and the oldest nestling was about a week old. Lemmings (all *Lemmus*) were banked high on the north side of the nest in a half-circle and a few along the south side completed the circle. There were 83 individuals. Several were scattered as far as two feet away from the nest bowl, and one was in the nest among the young and eggs (Fig. 9).



FIG. 9. Snowy owl nest near Barrow, Alaska, as seen on June 26, 1953, containing five white young and four eggs more or less covered by them; surrounding them are 83 lemmings, all *Lemmus*.

On July 6, when the nest contained 8 young, there were only about 10 lemmings at the edge of the nest, some obviously quite old. These were left alone, and we stayed at the nest only long enough to weigh the young. On July 15, five young were waddling in depressions between polygons and over flat areas up to 50 ft. away from the nest; four were still in the nest, and two of these left as we approached. The largest of the young were still docile and weights were taken relatively easily. On this date the nest mound was worn and trampled, with many small pellets about. There were only two or three dead lemmings. On all visits the parents were in sight and not far away, and neither of them was demonstrative. But in this respect, nesting pairs vary (Murie 1929), and at other nests we observed hooting, barking, and distraction display with a feline wailing by the adults.

*Nest 3.* This nest, with six eggs, was not found until June 26, but it was fairly clear already on June 3 that nesting was underway in the area. Not far from

the nest site, a pair had been observed on May 24 and 28, and the male performed a courtship display both times. On June 29, when the female was incubating, the nest contained only five eggs, the sixth being on the ground about two yards away. In late June, it was first noticed that the male of this pair was not regularly present. The female continued to attend the nest until at least July 8, but on the 13th, although a female, very likely the same one seen earlier, was present on a perch frequently used previously by the nesting birds, the nest was deserted. All six eggs were fertile. This nest was the most isolated of the three, and it is our opinion that disappearance of the male together with fairly persistent harassing by the abundant pomarine jaegers led to the abandonment of this nest.

From 31 eggs in five nests near Barrow in 1952 and 1953, only one or possibly two young were fledged. Human interference was responsible for the complete failure of a brood of eight young and possibly also four young and five eggs at two other nests, respectively. For the remaining losses of 14 eggs and young, we can only assume that natural factors were responsible. From the Hooper Bay area in 1924, Murie (1929) reported a substantial mortality of nestlings, estimated at about 50%. The impression left by our experience at Barrow is that here also reproductive success would prove to be low.

**Predation and food consumption.** All lemmings found at or seen carried to nests by snowy owls were Lemmus with the exception of one *Dicrostonyx* at nest 1 in 1952. Without a doubt, Lemmus comprises the bulk of the food of this owl, particularly of breeding pairs. But as preliminary examination of pellets shows, a variety of birds and also the least weasel (*Mustela erminea*) are taken. The size-range of prey taken among birds runs from lapland longspur to at least the old-squaw duck. These two species (and no others) were brought to nest 3 in 1952 in the course of a 48 hr. watch. Predation by the snowy owl on adult birds larger than the old-squaw is known (Murie 1929); some of these may be preyed upon when already injured or weakened, as are eiders (Wiggins 1953) and guillemots (Birulya 1907) sought on the ocean front along ice ridges in April and May. In general birds taken are smaller than an old-squaw (Murie *loc. cit.*; Sutton 1932).

Some evidence on food consumption during the nestling period was obtained in 1953 at nest 2. On June 26, most of the 83 lemmings accumulated at the nest rim were intact and fairly fresh. While these had evidently been brought recently, some soft and "ripe" specimens had clearly been on the nest mound for a week or two, as in the cold weather decay was slow. A few intact ones were torn, one was gutted, and from seven the head or both head and fore parts were torn. Of the 76 intact lemmings, 25 were females, 51 were males. From 75 of these weights could be taken, and the data are as follows:

Sex	Number	Total weight	Average weight	Range
Males.....	50	3887.8 gr.	77.8 gr.	54.9-102.1
Females.....	25	1758.4	70.3	37.9-104.4

Thus, adding a round figure of 50 gms for each of the eight additional carcasses, the total weight of lemmings at the nest was in excess of 6000 gms, or more than 13 pounds.

These are the facts from nest 3 as we found them on June 26. This nest was located at the edge of an area of high polygons with extensive marsh flats to the north and east. The male usually rested on a man-made low ridge north of the nest and apparently from here and from favorable hunting grounds over the marshes usually approached the nest to the south. This would explain the one-sided heaping of the lemmings. Also, it is possible that the accumulation was the result of increased hunting activity in the days following the start of hatching of the young. The large size of the lemmings taken reflects the fact that in late June, summer-born lemmings are not yet out, and the population consists of individuals born in the previous winter or earlier. The preponderance of males is likewise significant and fits in with other data obtained on lemming populations.

The total weight of the lemmings available for the female and young at nest 3 on June 26 becomes less impressive when one realizes what quantity of food must be consumed by this and other large owl families as the young are growing. Some indication of what this consumption must be is given by the following weights:

Nestling	June 26	July 6	July 15
1.....	199 gms	735 gms	1317 gms
2.....	141	625	1091
3.....	113	615	1049
4.....	66	408	971
5.....	51	347	900
6.....	Egg	246	855
7.....	Egg	185	678
8.....	Egg	119	524
	570 gms	3280 gms	7385 gms

The consideration of these totals should take into account also the average weight of a female owl, 2100 gms (Table 4), inasmuch as she normally draws on the supply of food brought by the male, at least early in the nestling period.

A young owl from nest 2, still unable to fly, was placed in an outdoor cage near the laboratory on July 21 and a daily record was kept of its weight and food consumption. It was then about four weeks old. All food provided consisted of Lemmus except a red phalarope weighing 66 gms given to the owl in the interval between weighings on August 18 and 19. The owl was weighed each day at noontime. In the period July 21-August 1, its weight increased from 1079 to 1676 gms (Fig. 10). It was fed 3 to 9 lemmings daily, average 5 (weighing 298 to 822 gms, average 451.2 per day). After July 1, weights fluctuated from 1568 to 1731 and averaged 1662 gms. The owl received 3 to 7 lemmings daily, average 4 (weighing 74 to 486 gms, average 326.4 per day). The first successful flight of this owl occurred on August 13.

Up to August 4, only large lemmings, from 60 to 112 gms, were offered to the young owl. On August 4 and later, the lemmings provided included young



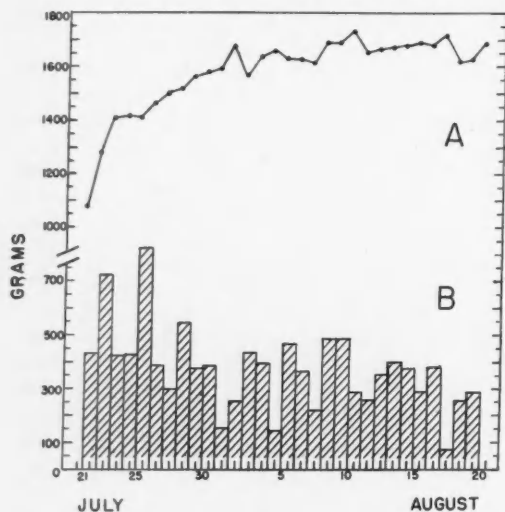


FIG. 10. Record of daily weights of a young snowy owl (A) together with weights of lemmings fed to it between weighings (B).

(from 18 gms up) as well as adults. Individual lemmings were gulped entire or torn in the course of feeding. On August 11, a lemming weighing 85 gms was swallowed and coughed up twice but retained after the third swallow. That the owl can ingest a lemming of this size comfortably, however, is indicated by records of an 87 gm lemming taken on August 10 and a 103 gm lemming taken on August 5, both swallowed entire without difficulty.

Thus, after the owl stopped gaining, an average daily weight of 1662 gms was sustained by an average daily consumption of 326 gms of lemmings (or about 20% of the body weight). A daily catch of four well-grown lemmings would therefore provide this young owl with an adequate diet.

It is clear that a family of snowy owls draws heavily on a lemming population. If the family of nest 2 had survived with five or six young, these with their parents would require several dozen lemmings daily if they were all to thrive. It seems almost inevitable that the food requirements of snowy owl families can meet with only partial success, under the circumstances prevailing near Barrow at times of lemming abundance and in other similar parts of the arctic, because midsummer populations of lemmings are depressed and because a number of predator species are exploiting the same prey. Even territories of 2-4 sq. mi. mean that nesting owls face a high probability of food shortage. Hence the surmise of low nesting success ventured earlier becomes the more reasonable.

### 3. SHORT-EARED OWL

In the Barrow area, the short-eared owl is reported by Bailey (1948) to be common "at times." This implies that the short-ear does not vary there so consistently in correlation with numbers of lemmings

as do other predators such as the pomarine jaeger and snowy owl. This was indeed suggested in 1953 by the remarks of Eskimos who indicated that this owl was not one regularly familiar to them. One middle-aged and observant Eskimo with whom we frequently talked about birds said he had never before seen the egg of a short-ear. Moreover, Bailey, reporting on a number of years of collecting near Barrow, lists only four nests found there, whereas in 1953 we found 28, and this was by no means the total number of nests on the area studied by us. For the short-ear as for the pomarine jaeger, McIlhenny (Stone 1900) obtained a series of 11 specimens in the period June 2-22, and this again suggests that the season of 1898 may have been similar to that of 1953. [McIlhenny probably obtained eggs of this species, also, but we cannot find any published report other than that of Stone (*loc. cit.*) dealing only with specimens of skins. Bailey (1948), in describing the scope of his work, makes no reference to collections of McIlhenny.]

*Relative numbers.* In 1951, no short-eared owls were seen. In 1952, one was seen on June 15 flying across marshes near Elson Lagoon, and none was recorded after that date. In 1953, however, the species was common, nesting at many locations and apparently throughout the Barrow region.

The first short-eared owl in 1953 was seen on May 24, when one used as lookout perches 25 and 15 ft. masts on the tundra just south of the Navy Base. On May 25 at least 3 and probably 5 different individuals were seen near the Base. On May 26 definite evidence of predation on Lemmus was obtained. On June 4, during a survey trip over the high tundra south of Barrow Village, three separate pairs were observed. On June 5, 8 to 10 individuals, or 4 to 5 formed or forming pairs, were on wing and spaced out along the length of census plot 1 (2 x 20 ac.) on the old beach ridge, and additional pairs or individuals were present in surrounding areas. Active aerial display, aggressive calling, hooting, and chasing were witnessed. Active territorial strife occurred among neighboring birds. In the same area later on June 5, two pairs were perched near spots used a few days later as nest sites; two other pairs were probably present at this time, also, but at any rate, all four pairs were seen on June 8 and subsequently on a succession of dates. The nests of these four pairs were located after the 8th on the 40 ac. plot.

Following the influx of owls in late May and early June, their general occurrence over the tundra was evident only in the first week of June when considerable time was spent by them on wing in display and territorial behavior. In subsequent weeks, owls were found only as they were flushed by chance during various traverses of the tundra or in the course of systematic coverage of census plots and their surroundings. Hence, an over-all density figure cannot be given for the short-eared owl. But it may be stated with confidence that the density did reach 7 pairs per sq. mi. on the mile-square unit including census plot 1 and most of plot 3 (Fig. 4). On the



basis of all other nests and locally occurring owls found elsewhere in the survey area (17 nests and presumed pairs), it is our impression that the over-all density was at least 3 or 4 pairs per sq. mi.

The smallest territories were of the order of 50 ac. Some were possibly even smaller, at least in mid-June when the population was densest, because these owls favored the more broken, better drained parts of the tundra, along ridges and in areas of polygons, and avoided extensive marshy flats.

After nesting started, and in the course of the remainder of the summer, numbers of short-eared owls slowly fell. Pairs whose nests failed did not remain in the vicinities of their respective nest-sites. These small owls were harassed persistently by jaegers, one owl often having to cope with both members of a pair of jaegers. It seems likely that the general interference of the jaegers was a significant factor, if not the chief one, causing the local exodus of the short-ears.

There is no indication that in the previous lemming cycle near Barrow, short-ears were as numerous as in the most recent one. Short-ears were not recorded near Barrow in 1949, but one was seen on May 25 on Wainwright Inlet (about 100 mi. WSW from Barrow) when Lemmus was very abundant there. In 1950, in the Barrow area, the only record is that of one seen near Nuwuk on May 30 (R. Rausch). In 1954, no short-ears were reported.

*Nesting cycle.* The nesting cycle at Barrow spans at least 11 or 12 weeks. In 1953, short-ears began to arrive near Barrow in the last week of May. Pairing and occupation of territories occurred in the first week of June. Clutches of eggs were begun at or near the end of this week. The first young found was hatched on July 6 from a clutch the earliest egg of which we estimate was laid on June 6. All other hatchings occurred later. Thus all indications are that incubation requires longer than the 26 days recorded for mid-latitude short-ears (Witherby), and the incubation period is probably 28-30 days (Pitelka *et al.* 1955).

As in the snowy owl, only the female incubates and broods. But both parents care for the young.

What records we have indicate that the nestling period may vary from 16 to 31 days. Our first record of a young bird in flight was August 8, somewhat later than might be expected from mid-latitude data. The period of dependence after young take wing is apparently unknown. At Barrow, we were unable to observe young in late stages of development, but in the light of all available evidence, it is unlikely that any would have become independent before the middle of August. On these bases, we arrive at the minimal estimate of 11 or 12 weeks given above. Evidence we have together with information from the literature in support of this estimate is discussed in detail elsewhere (Pitelka *et al.* 1955).

In all 28 nests were located, and clutch size was determined satisfactorily in 22 of these. Clutch size varied from 4 to 8, and the distribution was as follows:

Size of clutch.....	3	4	5	6	7	8	9
Number of records.....	0	2	3	6	8	3	9

This averages 6.3. The breeding performance of these owls at Barrow in a year of lemming abundance is comparable to what is regarded as "normal" at mid-latitudes (Witherby *et al.* 1940). According to Schaaning (1907), in Ost-Finmark, clutch size is normally 3 or 4, but in lemming years, reaches a maximum of nine. In years of vole plagues at mid-latitudes, clutch size increases to 9-14, and two broods may be raised. At arctic latitudes, only one brood may be raised. Also, there was no indication, at Barrow in 1953, that any re-nesting efforts occurred for those pairs whose nests were unsuccessful.

Of the 28 nests, two were observed only in early egg-laying stage. In 26, clutches were completed. One nest was seen with completed clutch after July 1 and only once. Of the remaining 25, 11 were disturbed in one way or another and deserted before any eggs had hatched. Of the remaining 14, three were deserted when only part of the eggs had hatched. Thus surviving nestlings were produced in 11 nests. Of nine of these, six were at least partly successful and three were apparently completely successful, by which is meant that all young were raised at least to the point of leaving the nest. Two, found on July 30, were empty, but showed signs of occupancy by young and were presumably at least partly successful. Thus, on the basis of unit nests producing at least one nestling or fledgling surviving through the incubation period was 14/25 or 56%. Survival through the nestling period was possibly as high as 11/14, and at least 9/12. For 23 nests with adequate data [28-(2+1+2)], only 3 or 13% were completely successful, but the number of nests which each produced at least one young leaving the nest was possibly as high as 11/22 or 50%.

For 21 nests, histories of 133 eggs are summarized in Table 2. Loss of eggs before hatching was 51.9% (69/133). Loss of eggs and young through the period of hatching was 67.7% (90/133), and unhatched eggs in successful nests raise the loss estimate to 70.7% (94/133). Percent of eggs producing young was therefore 29.3% (39/133). Success of young leaving the nest was at least 12.8% (17/133), or 43.6% of those hatched (17/39). At the first of two nests found by I. L. Wiggins near Dry Lake on August 1, there were five young scattered within 20 yds. of each other; in the second there were two young. These additional records with those of Table 1 lead us to believe that fledgling success (number of young taking wing) was probably of the order of 5-10%.

On the basis of hatching records and examination of eggs from deserted nests, 72 of 80 eggs (in 13 completed clutches) were normal. Two contained abnormal embryos. Six were infertile. Thus the fertility rate was at least 92.5%.

Of three nests destroyed before eggs hatched, puncture marks on one or more of the remaining eggs pointed to pomarine jaegers as the predators. At a

TABLE 2. Data on nest success of the short-eared owl near Barrow, 1953.

	Number of nests	Number of individuals
Number of eggs.....	(21*)	133
Loss before hatching.....	11	69
		64
Loss during hatching.....	3	21
		43
Infertile eggs (3) and fertile eggs (1) unhatched in otherwise successful nests.....	..	4
Young hatched.....	7†	39
Number observed alive away from nests.....	..	17
Additional nests which were partly or completely successful.....	6	
Minimal number of young known for four of these six:		
Still in nest.....	..	6
Left nest.....	..	5
Nests with histories unknown.....	3	
Total number of nests.....	30	

\*This figure, not to be added in this column, is the number of nests containing the total of 133 eggs. These 21 plus one complete clutch of 6 with later history unknown provide the 22 used to calculate average clutch size.

†This actually includes young hatched in 6 nests and 2 young with 4 eggs in a seventh nest; when the latter was again visited, after young had left, condition of the nest bowl and surroundings suggested the nest had been successful.

fourth nest, which contained seven eggs on June 29, there was only one chick and one egg on July 13, still covered by the female. The chick, though still alive, had the skin over its occiput torn and its left leg was badly bitten. At a fifth nest, with eight eggs on June 21, clutch size fell progressively to five by July 29, when the female was still incubating, but on July 5 this nest was abandoned still containing five eggs. This additional evidence of losses at the nest also points to the pomarine jaeger, although we never witnessed a jaeger molesting an owl's nest. Evidence of predation in the period when young are away from the nest was observed on August 8 when a well-feathered young, one of seven which had left their nest successfully, was found partly eaten.

In less obvious ways the pomarine jaeger may have been a factor in the drop-off of breeding owls which occurred through the summer. If the male owl is responsible for food required by the female and nestlings, even if only for a part of it, there is the possibility that some nest losses occurred because of chasing and harassing by jaegers which led to exposure of nests when females left them. Attacks of jaegers occasionally caused an owl to fly distances well beyond the reasonable limits of a local living area or territory, under circumstances of population density prevailing at Barrow in 1953.

**Predation and food consumption.** Although short-eared owls are known to prey on a variety of small birds, including longspurs (Saunders 1923) and snow buntings (Errington 1932), we found no evidence near

Barrow that they were preying on anything but brown lemmings. This statement is based on observations at and near nests and elsewhere in areas where short-eared owls were present and were suspected or actually observed to be responsible for some of the remains of lemmings which we found. Pellets of this species were not collected by us. At certain localities of more southern latitudes, the nesting of this owl is also considered to be dependent upon the local abundance of a microtine, for example, *Microtus agrestis* in Britain (Armstrong & Phillips 1925; McWilliams 1941; Elton 1942). Elsewhere, however, the prey taken by breeding birds is various (Errington 1937).

Lemmings caught by short-eared owls are apparently decapitated or torn in two if too large, and only the body may be ingested. This we surmise from finding heads, or heads with viscera attached, at or near places where short-eared owls were perched or from which they were flushed. What prey we observed at nests also consisted only of Lemmings.

A young short-eared owl out of the nest but still unable to fly was brought to the laboratory on July 28. At this time its wing and tail feathers were partly grown, although the latter had only recently burst through their sheaths. The owl may have been about three weeks old. A record was kept of its weight taken daily early in the afternoon and of the weight of lemmings offered as food (Fig. 11). The owl reached a maximum weight of 404 gms on August 4, after daily consumption of 4 to 14 lemmings, average 7 (90 to 298 gms, average 164 gms per day). After the 4th, its weight varied only moderately, from 343 to 387 gms, average 358 gms. It was fed 3 to 7 lemmings per day, average 5 (96 to 214 gms per day, average 127 gms). Weight of individual lemmings varied from 15 to 35 gms, but occasional ones reached 50 gms, and one weighed 73. These were torn and all parts were eaten.

The owl was kept out of doors, in a roofed cage which probably provided more comfort than any natural situation it could use while still unable to fly. Moreover, although the owl was supplied daily so that it was not without food, it temporarily ignored some portions of generous offerings and apparently ingested food at fairly regular rate. Hence, one would expect that the daily consumption of 127 gms is not far above the minimum requirements. Average daily weight of about 360 gms after the initial period of weight gain, thus, was sustained by an average daily consumption of 125 gms (approximately 35% of body weight). This seems to be an exceptionally high food intake/weight ratio but no error can be detected in the field data.

Chitty (1938), using an adult Short-eared Owl which varied from 425 to 478 gms in the period of his study, determined that it consumed 62 to 118 gms per day when excess food was continually present, only 51 to 75 gms per day over the whole period of observation (February 20-July 1). Thus, our owl, a youngster in a cold climate, weighing about 100 gms less, was consuming up to 75 gms more per day. Only for 3.2 days (March 16-19) when Chitty's owl was

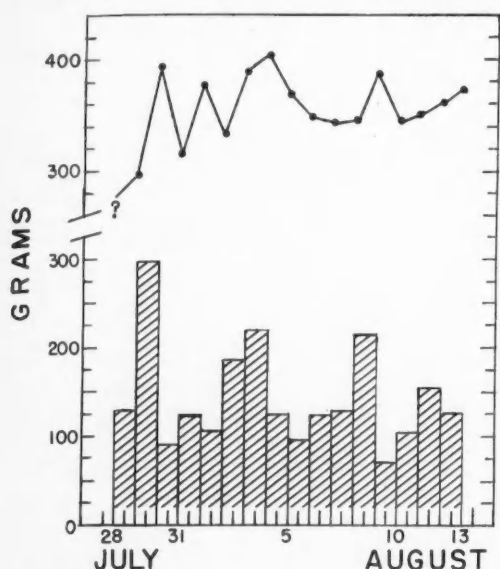


FIG. 11. Record of daily weights of a young short-eared owl (A) together with weights of lemmings fed to it between weighings (B).

taking 118 gms/day were the rates of the two individuals similar. The difference seems reasonable, first, because our owl was a fledgling, attempting flight only at the close of the 16 day study and, second, because prevailing temperatures were probably considerably lower than those to which Chitty's (Oxford, Eng.) owl was exposed. Thus, extremes of air temperature recorded at the Barrow, Alaska, airport in the period July 28-August 13 were 28 and 67° F, and the daily means varied from 32 to 53° F (average, 39.9° over the 17 day interval). Available food for the growing owl must sustain normal processes of both maintenance and development, and in addition, its immature and indeed incomplete plumage is no doubt less efficient in heat conservation than the plumage of the adult.

## MINOR PREDATORS

### 1. LONG-TAILED JAEGER

On the basis of both our records and the literature, it appears that the long-tailed jaeger is relatively unimportant as a predator in the Barrow area. Records for the Barrow area summarized by Bailey (1948) indicate that in some seasons the species may be more common than found by us, but this is apparently true only of occasional seasons and in any event the species has not been found nesting on the coastal flats near Barrow. It breeds in the interior, as Bailey (*loc. cit.*) reports, but data from eggs collected formerly are not exact or dependable enough to show how close to the coast breeding occurs.

In 1951 and 1952, this species was scarce. In 1951, it was recorded on but four days, July 3, 7, 15, and 17. On the first, a loose flock of ten was found on

census plot 2, and five of these were collected, three males and two females. Of these, two males were first-year birds; all others were adults. In both females, examination of ovaries ("regressing") and abdominal skin ("brood patch developed") indicated that they may have at least begun nesting elsewhere; at any rate, these were either non-breeding birds or any attempted nesting had been a failure. On the 7th, a group of 11 moved north across plot 2 following the shore of Elson Lagoon. On the 15th and 17th, two and one individuals were seen, respectively.

In 1952, the only long-tailed jaegers recorded were one seen on July 15 near the Navy Base and four seen on August 11 near Lake Ikroa-vik, 6 mi. south of the Base. This species was found by Treichel on August 2 to be the most common jaeger in the delta of the Colville River on the arctic coast 150 miles east of Barrow.

In 1953, although more common than in either of the previous two summers, the long-tailed jaeger occurred irregularly from June 7 to July 19, in which period it was noted on nine different dates. On each of three of these, a pair was seen; otherwise only single individuals were recorded. On two occasions pairs were persistent in remaining in given areas and disputing them with pomarine jaegers, but no clear indication of nesting effort was observed. An adult male collected from a pair on June 15 had well-developed testes (13 mm in length).

### 2. PARASITIC JAEGER

It appears that like the long-tailed jaeger, the parasitic jaeger figures only incidentally in the overall predator-prey ecology of the Barrow area. While *parasiticus* may breed in the Barrow area, there is no indication that it does so except in small numbers and merely occasionally (Bailey 1948). It is interesting that the only breeding recorded near Barrow in 1951-53 (one nesting pair) occurred in the year of lower abundance of breeding pairs of *pomarinus* and that in the year of higher abundance of the latter species, not only was there no breeding of *parasiticus*, but indeed the species was less common than in either of the two previous years. Schaaning (1916) and Bertram *et al.* (1934) also suggest that *parasiticus* may fluctuate inversely with abundance of other predators. Aggression of pomarine jaegers toward all other jaegers as well as other avian predators utilizing lemmings is such that competition with its larger congener is probably a factor in local occurrence of *parasiticus*.

In this connection, some observations in the foothills of the Brooks Range are relevant. In the period July 31-August 7, 1951, at East Oumalik, 110 mi. south of Barrow, H. E. Childs, Jr., noted that parasitic jaegers were common and long-tailed jaegers less numerous, but also common. Pomarine jaegers were not seen. The two smaller jaegers present fell off in abundance toward the end of Childs's stay and apparently neither species was nesting then, since there was no evidence of locally established pairs caring for young they would normally have in late July and

early August. However, from an earlier visit to the same area, in mid-July of the same season, H. W. Setzer reported *parasiticus* was nesting there.

In 1951, parasitic jaegers were seen from June 9 to July 21 on 17 different days. Their occurrence was scattered and brief, and they were observed wandering singly, in two's or in three's. Some of the couples were evidently pairs. One such remained on one part of the west side of Central Marsh over the period July 13-21. In 1951, of the three species of jaegers, *parasiticus* was the most frequently seen.

In 1952, parasitic jaegers were seen from June 13 to September 4. They were about as numerous as in 1951, but by contrast with that year, were present throughout the summer. A group of four on July 3 and one of five on August 17 were the largest groups noted in 1952. One nesting pair, and the only one in the survey area, located by D. Q. Thompson, was observed by us on several different days. The parasitic jaegers defended their territory against neighboring nesting pomarine jaegers, and their territories were evidently mutually exclusive. This is indicated also by observations of Salomonsen (1951).

In 1953, this species was distinctly less common than in the previous two years. It was recorded from June 11 to July 28, and in this period single birds were seen on seven different days. In addition, one pair was seen at Barrow-3 on June 16. A male found on June 28 with an injured wing was otherwise in good condition, with moderate deposit of subcutaneous fat (weight, 354 gms; testis length, 12 mm).

#### GLAUCOUS GULL

The glaucous gull normally occurs on the arctic coast from early May to early October (Bailey 1948), and it was present during all periods of our field work near Barrow. This gull is apparently attracted to tundra areas near the coast in late May and early June when lemmings are abundant. This of course occurs before large inland lakes and coastal lagoons are open, and at this time, except for what man may provide, the gull relies on food available along the open leads. But on adjacent tundra, because lemming remains may be left by both snowy owls and pomarine jaegers, the gull can scavenge. It apparently catches lemmings, also, working on the ground.

In the last week of May, 1953, a few gulls were noted on each of several dates resting on the tundra in places normally not attractive to them. That they were feeding on lemmings became clear on May 29, when small groups of two to five were found scattered over the tundra in the course of a survey south of the Village and Base. Numbers of jaegers were then estimated at 2-3/sq. mi. It was noted then that gulls were several times more numerous than jaegers, and 5-10/sq. mi. is probably a conservative estimate. We frequently found gulls' tracks at open lemming burrows in the snow and particularly in areas of partial melt-off where the receded snow had revealed

the extensive burrows and feeding areas of the lemmings. While we never actually saw a gull seize and lift a lemming, several times the quick movements of gulls watched at a distance suggested they were actively attempting to catch living lemmings.

In the course of such foraging, gulls evidently come into conflict with both owls and jaegers. On May 29, 1953, two gulls and an owl were watched in a melee in which the owl pursued one gull in circular flights up to 50 or 75 ft. above the ground and then back down to the ground. The gull was then pursued on wing again, but after a distance of a quarter mile or so, the owl stopped its chase and turned back. The pursued gull was carrying a dark object in its bill, almost certainly a large lemming. On the 29th, also, jaegers chased and harassed gulls. This also happened many times on breeding territories in the course of the summer when occasional gulls merely flying over the tundra would cross such territories.

In 1953, jaegers became abundant on June 1, and on that date only one group of three gulls was seen standing and walking about on the tundra, in the course of a trip over much the same areas visited on May 29. Such groups were not recorded after that date. These facts combined with the general absence, in 1951 and 1952, of gulls on tundra areas in late May and early June indicate that in years of lemmings abundance, the glaucous gull may actively prey on lemmings and may be important before the primary predators take over the area.

In 1953, in the week beginning June 4, snow melt-off proceeded rapidly and many lemmings moved as scattered, wandering individuals off tundra areas onto coastal gravel beaches and out on the ocean ice. They were concentrated locally only on the beach where they sought food and shelter around and in islands of herbaceous vegetation. It is very likely that many of these lemmings, particularly the individuals out on the ice, fell prey to gulls. The gulls could also be expected to scavenge on the dead or dying ones seen by us along the ocean shore in this period.

Similar observations were made by I. L. Wiggins (pers. comm.) on June 23, 1952, when a group of 6 to 8 gulls was watched on an area of high polygons where snow patches were still present. The gulls' movements on foot and their intermittent short, low flights clearly suggested they were hunting for lemmings. Likewise, in the spring of 1949, R. Rausch (pers. comm.) noted gulls feeding on the ground in areas where lemmings were known to be present and dying; he inferred the gulls were feeding on lemmings. T. Cade, however, reports definite evidence of microtine remains in stomachs of glaucous gulls taken along the Colville River.

Manniche (1910) mentions that the "arctic gull" (very likely *Larus hyperboreus*) is a lemming predator, and Tcherniakofsky (1939) cites Eskimo reports to the same effect. No more definite particulars in the literature have been located. Elton (1942) cites reports of *Larus ridibundus* preying on voles.



## DISCUSSION

## 1. TIMING OF BREEDING EFFORT IN RELATION TO BREEDING SUCCESS

Comparison of the nesting cycles of the three avian predators important near Barrow Alaska, brings out the fact that while they respond to a food supply sufficient to initiate breeding, a fairly prompt beginning to this effort is essential if it is to be successful. This is so apart from the need for sustained availability of food. As a basis for the ensuing discussion of this and other aspects of timing, the chronologies of the nesting cycles are summarized in Fig. 12.

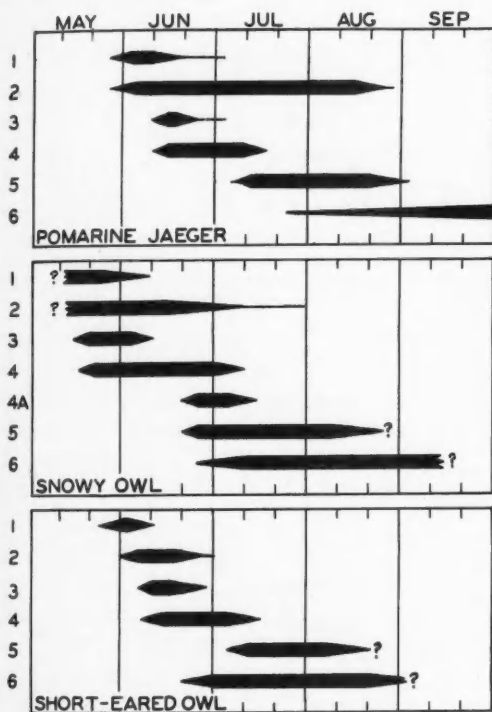


FIG. 12. Generalized chronology of nesting cycles of three species of avian predators near Barrow Alaska, showing time taken by various stages and their relation to molt. 1, pairing and territorial establishment; 2, territorial behavior; 3, egg-laying; 4, incubation; 4A, egg-hatching; 5, young dependent (precocial in the jaeger, altricial in owls); 6, annual molt of adults.

In the pomarine jaeger, egg-laying may occur in the Barrow area (lat. 71°N.) over as long as 20 days (June 10-July 1,  $\pm 1$  or 2 days, in 1953; but only 5 days, June 20-25, in 1952). For the Barrow area, Bent (1921) reports 36 egg dates from June 12 to June 27. The chief period of egg-laying is evidently June 15-25. This appears to hold for other parts of the American arctic where *pomarinus* breeds, for example, on Southampton Island, lat. 64°N. (Sutton 1932). Near Hooper Bay (lat. 61°N.) Brandt (1943) found a complete set as early as June 9 and ten others

were found between that date and June 22. Dates for the Eurasian arctic (Pleske 1928) run from June 13 to July 5, and for Novaya Zemlya (lat. 73°N. where observations were made), Schaaning (1907) reports first eggs of nine sets laid in the period June 26-July 14, in 1903. Thus, while the latter half of June is the period in which eggs are generally laid, and while year-to-year variation is of course to be expected, there is some indication that the period of egg-laying is later, on the average, at higher latitudes. This is in fact shown for *parasiticus* by Dementiev *et al.* (1951). Also, it is clear that in this as in other arctic species (Pitelka MS), breeding effort may continue so late in the summer that failure of the late nestings is inevitable merely because, in the case of jaegers, there is not time for the young to be fledged successfully.

In the snowy owl, the nesting cycle requires a period longer than that of the jaeger or short-eared. Yet first-egg dates reported by Schaaning (1907), Pleske (1928), and others run from May 28 to June 10, with a few exceptional dates as late as June 28 reported by Schaaning. Such a wide time latitude of breeding response at first suggests that timing factors may not be so critical in this species, but the facts appear to indicate otherwise.

In the first place, accessibility of prey with relation to snow cover as well as its relative abundance appear to be factors in the inception of breeding. On the basis of an incubation period of 32-33 days (Pleske 1928; Murie 1929; Witherby *et al.* 1940), first eggs at two nests in 1952 observed after clutches were completed were laid in or close to the period June 5-10. In addition, a third nest found on June 7 then contained only one egg, and on the same date the pair at this nest was observed in copulation. In 1953, first eggs in two nests were laid in or close to the period May 15-20. The season of 1952 was delayed, with heavier than usual snow cover in late May and early June, and the difference in inception of breeding which our observations indicate probably reflects this. In 1952, also, lemmings were less numerous than in 1953.

As in the jaeger, owl nestings started late are probably certain to fail, and in fact there is reason to believe that timing factors set a limit on the clutch size in populations of this species at high latitudes. Several writers (Pleske, Sutton, Schaaning, and Salomonsen) do not report clutches in excess of nine or ten (Table 1), and the reports of clutches reaching 13 to 15 may be open to question. We note that Bailey (1948) is careful to attribute reports of such large clutches from Barrow to the collector Brower, and the largest clutch reported by Bailey himself is nine. It seems dubious whether the female could effectively cover so many eggs. Also, it seems even more dubious whether in a species with so protracted a nesting cycle, clutches could be so large because hatching would then spread over a month and for the last five or so individuals failure would be virtually certain. If (for example at Barrow) the oldest in-



dividual from an early nesting does not take wing earlier than about August 10, it is difficult to see how the time available before sleet, snow, and falling temperatures come could allow for more than ten young. This presupposes that clutch size and number of young would evolve to the average maximum number which the adults can raise (Lack 1947), not only in terms of food available but also the time available. At any rate the facts as presented, in the owl as well as other species such as jaegers, may disprove some of the claims made for especially large clutches in arctic birds. This matter deserves critical attention in the field. Also, it is now self-evident that late clutches can fare no better than the last eggs of exceptionally large clutches.

In the short-eared owl, length of the nesting cycle at 11 or 12 weeks similarly sets limits on breeding success of the population. Thus, in the latest nest found by us, the clutch was started on June 21 or 22. This nest was later found destroyed. According to the time estimates discussed above, adults of this nesting would still be attending young in the first and second weeks of September. The prospects for such late attendance upon young to occur near Barrow are dim indeed.

Still another complication affecting both timing and ultimate success enters. The complete annual molt overlaps nesting activities of all three species, and hence food requirements are increased by this regular phase of the annual cycle. In the pomarine jaeger, molt begins in at least a part of the population while nesting is still underway, in late July or early August, two to three weeks after egg hatching (Fig. 12). Thus, molt proceeds for as much as four to five weeks while care of surviving young is being concluded. For the two owls, however, molt is population-wide and also begins earlier than in jaegers. In the snowy owl, it gets underway in late June, as observed by us and also by Dementiev *et al.* (1951). In the short-eared owl it also begins in late June, and by the 20th of that month in some individuals. Thus, for the snowy owl and the high-arctic short-eared owls, molt starts while the female is still incubating. Molt then proceeds through the summer and is apparently largely completed before any major post-breeding movement, which for the short-eared owl means a considerable southward migration. These circumstances give us another reason why, in the short-eared owl, re-nesting of unsuccessful pairs may be out of the question even in the absence of a locally settled common and persistent predator like the pomarine jaeger.

It is interesting to realize that the two of these three predators characteristic of the high arctic, the snowy owl and pomarine jaeger, protract their breeding effort when lemmings are abundant. For reasons given above, such late nestings cannot be successful and indeed the adult owls may run some risks, so to speak, if the energy demanding molt process is delayed and pushed back into an autumn period when food may be scarce. Protraction of nesting effort was true of the 1953 jaeger population and apparently also of the dense snowy owl population observed

in 1903 on Novaya Zemlya by Schaaning. As is shown in the summary table of Pleske (1928), some clutches recorded by Schaaning were not started until the last days of June, and Pleske estimated that the last young would hatch around August 10th. It is difficult to see how these broods could be successful. One is left with the impression that in the presence of an exceptional abundance of lemmings, the predators can become somewhat reckless, so to speak, expending effort in breeding a substantial part of which is evidently futile. This applies also to the late-nesting jaegers reported by Schaaning.

Finally, timing of breeding effort also bears a relation to change in numbers of the prey itself. When the snow melts in early June, the exposed lemmings are literally pounced upon by an influx of predators whose populations must then adjust as the density of prey falls. This adjustment was clearly seen in the commonest of the predators, the jaegers, and was particularly evident in 1952 when lemmings were only moderately common. That part of the jaeger population which remained and bred then enjoyed an augmented supply of food when the summer generation of lemmings began to appear above ground in mid-July. This increase, however, did not bring the supply anywhere near the early summer levels, in either 1952 or 1953. Thus, lemmings with low reproductive rates (1953) or virtually non-reproducing (1952) in early June, begin large-scale breeding as the snow melts off and the young appearing in mid-July not only relieve the tightening food situation for the adult predators but provide food for the young jaegers and owls then hatching. In 1953, when both lemmings and predators were more abundant and breeding was not so sharply timed in either group as in 1952, the relation of hatch to food increase was not evident; instead, by mid-July in 1953, deterioration of the predator-prey situation was evident not only from nesting failures and the number of non-breeders present, but also from a fall in reproductive rate of lemmings (Rausch & Pitelka, MS).

Thus, several factors act collectively to govern the progress of breeding of the avian predators. These are (1) the time required for nesting cycles if, under conditions of high arctic climate, the young are to reach a stage of at least semi-independence; (2) the intrusion, so to speak, of the molt process into the breeding period, aggravating the food situation and also acting to set a limit, in the owls, on the time when latest breedings can be started; (3) the June fall-off in prey numbers, limiting the density of predators undertaking breeding and then limiting the success of the latter; and (4) the mid-July boost to the food supply when the summer generation of lemmings appears at about the time eggs of jaegers and owls are hatching.

## 2. GENERAL STATUS IN THE ARCTIC OF AVIAN PREDATORS NEAR BARROW

The circumpolar distribution of the snowy owl and its importance as a predator in tundra communities

is well known. The relative importance of the other two major predators here considered, the pomarine jaeger and the short-eared owl, is not so clear.

The short-eared owl is known as a breeding species from high latitudes (Witherby *et al.* 1940), and its occurrence as such in tundra areas is probably fairly extensive if Bailey's (1948) summary for northern Alaska may be taken to indicate the situation generally. Nonetheless, breeding may be sporadic or irregular, even regionally. In the Barrow area, the short-ear occurs irregularly and perhaps this is more or less true for arctic coastal plains. In the interior, at Umiat, on the Colville River, it was noted in three successive summers, 1951-1953, and as at least a sparse resident the short-ear may be present there more regularly. Pleske (1928), while reporting that the short-ear has been recorded nesting in Eurasia from Russian Lapland eastward, states only that it was "noted in small numbers." It is true that in Taimyr, for example, Birulya (1907) did not definitely identify it, but other writers indicate that the species is probably more common than stated by Pleske (Schaaning 1907; Zhitkov 1912; and Mikhel 1935). In parts of the American arctic, as north-eastern Labrador, the short-ear nests at least occasionally (Hantzsch 1908), but none of a series of other reports for that area cited by Austin (1932) suggests the species is ever common. In Greenland, the Short-ear occurs only as a straggler (Salomonsen 1951), and there are no reliable records from Baffin Island (Soper 1928 and 1946). It was not found on Southampton Island by Sutton (1932).

That presence of short-ears in arctic areas may depend upon the abundance of lemmings has been stated by Bailey (*loc. cit.*). The possibility of large-scale breeding of this species in conjunction with peaks in lemming numbers is suggested by such records as those of McIlhenny (Stone 1900) from Barrow, Alaska, and of Popham (1897) who reports the short-ear to be the commonest owl along the Yenisei River in a year when there was "a large supply of lemmings on the tundra"; but apparently it was rare or absent in the years 1897 and 1900 (Popham 1898, 1901). Records of short-ears becoming common with lemmings in the American arctic have been found by us to date from but one area: Taverner & Sutton (1934) and also Shelford (1943) report this species as common and nesting near Churchill, Manitoba, in 1933, a lemming year, but in the previous three years when lemmings were less numerous or scarce, short-ears were scarce or absent. In Europe, Collett (1894) mentions that short-ears become common on Norwegian mountain plateaus in lemming years, and Schaaning (1907) states that in Ost-Finmark, where the short-ear is common, clutch-size is normally only 3 or 4, but in lemming years it may be as high as 9.

The ability of the short-ear to respond to an abundant supply of microtines is well known in mid-latitudes, as Elton (1942) shows. He cites a figure of 40 nests on 3500 ac., which is equivalent to about 7 pairs/sq. mi. This order of local density is com-

parable to that at Barrow in 1953. The only out-and-out attempt to census a short-ear population known to us is that of Goddard (1935a, b). For one of two successive years of study, he reported a maximum of four nesting pairs on 2300 ac., or about 1/sq. mi. This, for a breeding population, would appear to be only a moderate density when compared with the record cited by Elton or that obtained at Barrow.

Thus, populations of the short-eared owl, while apparently playing only a variable role in the recurring lemming cycles, are able to participate in predation on lemmings in a conspicuous way, even so far north as 71°N. latitude, and to achieve breeding densities there roughly comparable to the highest known for mid-latitudes. One reason for the indefiniteness of the evidence concerning the short-ear in the arctic may be that this species does not occur side by side with jaegers and snowy owls except in the one year of a cycle when lemmings are especially abundant and then only in those periodic peak years when particularly high densities are reached. Thus, in the recent cycle at Barrow, short-ears were important in 1953, but absent in 1952; and they were not recorded in the course of the 1948-49 cyclic peak. It would appear that in those broad areas of the tundra life-zone which are continuous with and, as it were, buttressed by, continental areas of more southern latitude, it is most likely that populations of this widespread owl can "spill over" sufficiently to the north to figure in the picture of predation on arctic coastal plains.

The role of the pomarine jaeger as a lemming predator is more certain than that of the short-ear, yet Elton (1942) does not mention the former species once. All three species of jaegers are known to prey on lemmings. This fact considered together with their structural and behavioristic similarities and their overlapping distributions suggests that they are at least partial competitors. If ecological segregation occurs, what light would this throw on the role of each species as a lemming predator? Discussion of this problem is based on three sources of evidence: (1) facts of distribution; (2) circumstantial evidence buried in the reports of faunists concerning the relative abundance of the three jaegers; and (3) limited direct evidence, from the field, of interaction between populations of jaegers.

With respect to distribution, of the three species of jaegers, *longicaudus* is apparently the most consistently distributed through the circumpolar tundra zone. As a breeding species, it is territorial and occurs at inland as well as coastal localities, on well-drained ground and in hills or even in mountainous regions. In northern Alaska and other similar parts of the arctic, as on the Yamal Peninsula (Zhitkov 1912), *longicaudus* becomes more common as one moves from the coast into the interior, while *pomarinus* of the coastal flats becomes less common. The breeding of *longicaudus* depends in many parts of the high arctic on the availability of lemmings (Løppenthin 1943) but in southern parts of its breeding range it preys on other microtines as well.

By contrast with *longicaudus*, *pomarinus* has a more restricted breeding distribution. Between western Greenland and Novaya Zemlya, it is absent or only rare as a breeding species (Pleske 1928; Southern 1944), but to the east, from Novaya Zemlya and the Yamal Peninsula to northern Alaska and thence to western Greenland, it breeds commonly, at least in certain years. The breeding stronghold of *pomarinus* is that section of the arctic where tundra areas are most extensive and most continuous north of 70°N. latitude and where, therefore, the coastal marshy plains are most widespread. Such marshy flats are the breeding habitat of this species, as is indicated by our observations and also by reports of Popham (1897), Zhitkov (1912) and Brandt (1943) as well as by the coastwise terrain of localities from which breeding is reported. Like *longicaudus*, *pomarinus* is territorial and apparently dependent at least as much as *longicaudus* on lemmings to sustain its breeding. This appears to be true for all records of large scale breeding of *pomarinus*.

While Southern (1944) acknowledges that breeding in *pomarinus* may be governed by the abundance of lemmings, he leaves this point open after citing evidence which he stresses is not consistent. Our report from Barrow upholds Schaanning (1916) in correlating the breeding of pomarine jaegers with the incidence of peak years in lemming populations in coastal areas. Breeding in such areas in years between cyclic highs, as is reported by Bertelsen (1923), is not surprising since the valleys in abundance are not so deep in some cycles as in others. While no breeding was witnessed in 1951 near Barrow, some did occur in 1950 (I. L. Wiggins, pers. comm.) in which year lemmings were also scarce. Hence Bertelsen does not necessarily contradict Schaanning, as Southern (1944) suggests. Moreover, some parts of Southern's Table 2 do not stand up under critical scrutiny. Kumlien's records from Disko Island have already been dismissed by Salomonsen (1951). Birulya (1907; same as 1905 listed by Southern) is cited as contradictory because jaegers were common in coastal Taimyr in a year not supposedly within a lemming peak, yet Birulya cites but one breeding record, and from his account we gain the picture of coastwise wanderings of jaegers such as were witnessed by us in Barrow in 1951. Evidence from von Jordans (1925) cited but not commented upon by Southern is presumably also contradictory in the same manner as that of Birulya. According to Southern, von Jordans reports *pomarinus* as common, in 1924, whereas the nearest Norwegian lemming peak is 1922-23, but von Jordans (1925) also found the snowy owl common and reports many pellets which apparently consisted mainly of lemming and mouse remains. Scalon (1932:169) definitely did not himself find *pomarinus* breeding, but Southern does not mention this, and here as with other reports he cites, Southern stresses relative numbers seen rather than evidence on breeding. Thus, while more evidence is required to determine the degree to which breeding in *pomarinus* depends on lemming numbers, we con-

sider (1) that on this point Southern overemphasized and even misinterpreted some of the evidence he apparently regarded as negative, and (2) that the positive statements of Schaanning and others should be given more weight than he allowed them.

We come now to *parasiticus*, which differs from the other two in several respects. First, although *parasiticus* has a circumpolar distribution, its occurrence is more maritime than that of either *longicaudus* or *pomarinus*. On Spitzbergen and Bear islands (Jourdain 1922), on Jan Mayen Island (Bird & Bird 1935) and on Iceland (Congreve & Freme 1930; Løppenthin 1938), *parasiticus* is the common breeding species, *longicaudus* breeds only occasionally, *pomarinus* not at all. On the coast of Lapland, and on offshore islands, Pearson (1896, 1898, 1899) as also Hortling & Baker (1932) report *parasiticus* to be the most generally distributed species of jaeger, with only *longicaudus* occurring as an additional species at some localities. Also, *parasiticus* breeds through a latitudinal belt wider than that of either *pomarinus* or *longicaudus* (Southern 1943, 1944; Dementiev et al. 1951). While *parasiticus* may be territorial like the other two species, it is apparently more generally semi-colonial. Its breeding depends to some extent on lemmings in certain parts of its arctic distribution, as in Alaska (Nelson 1887), in northeast Greenland (Løppenthin 1932) and in Norway (Collett 1894; Elton 1942). This appears not to be so obligatory a relation as in *pomarinus*, and we do not agree with Southern (1944) who suggests that *parasiticus* may be effected in its breeding by abundance of lemmings more than is *pomarinus*. In fact, the impression left by the literature is that *parasiticus* is primarily a maritime species, breeding at arctic latitudes and also more southern ones, in semi-colonial units on islands and coastal flats, from which individuals range out to prey on colonial seabirds and marine animals (Schaanning 1907). According to Pleske (1928), in Eurasia *parasiticus* is the most prevalent of the three species in western sectors, east to the Franz Josef Archipelago, the Murman Coast, and Kolguev Island. This is the main gap in the circumpolar distribution of *pomarinus*; it is also a gap in the distribution of extensive tundra flats. Here, then, and on parts of the northern rims of the Atlantic and Pacific oceans *parasiticus* breeds, if not more abundantly than elsewhere in its breeding range, at least more consistently. Southern (1943) does not acknowledge Pleske's statements about differential distribution of *parasiticus* in Eurasia, but Pleske's review of the literature was much more exhaustive than that of Southern, and what Pleske stated is a reconcilable detail of the generalized picture to be ventured later.

To consider now circumstantial evidence from reports of faunists concerning relative abundance of the species of jaegers, it is necessary first to acknowledge that the three may be sympatric in local breeding distribution. In North America this is definitely true for given years in such areas as Hooper Bay (Brandt 1943) and Southampton Island (Sutton

1932.) It is almost certainly true also for other parts of the arctic. All three species are known to breed in Greenland on the central west coast, on Disko Island and the adjacent mainland (Salomonsen 1951). Their breeding distributions also overlap in Eurasia (Dementiev *et al.* 1951), and the summary tables of Pleske (1928) repeatedly suggest local sympatry, but he does not give conclusive evidence. That it occurs is indicated by Popham (1897), who reports nesting of all three species on the Yenisei River in 1895.

Pleske's summaries (*loc. cit.*) suggest that in a given area either *pomarinus* or *parasiticus* is conspicuous as a breeding species, but not both, and that *longicaudus* may occur in fair numbers with either of them. This is a point buried in his tables and one to which he made no reference. Still other sources show (Bailey 1948, in combination with other sources on the Alaskan Arctic) that year-to-year changes in numbers of jaegers are marked. Moreover, we are unable to find any report of extensive breeding of both *pomarinus* and *parasiticus* in one area, in one season. Both at Hooper Bay and on Southampton Island, in the years mentioned above, *pomarinus* was third in order of general abundance and only local in its breeding distribution. Brandt (1943) comments that at Hooper Bay in 1924 *pomarinus* was unfamiliar to Hooper Bay natives; he suggests it may breed there irregularly and only when lemmings are abundant. On Southampton, in 1930, lemmings were also abundant.

Thus, the available literature concerning relative abundance and incidence of breeding in various areas shows that *parasiticus* has a regional breeding stronghold in the North Atlantic and the European section of the Arctic Ocean, but that in other parts of the arctic where all three species may occur commonly, some interaction between species with respect to their population densities may occur.

As to direct evidence on this interaction, there is little. Our thinking on this problem originated in the field when, by 1953, differences between the three successive years and the overlap of *pomarinus* and *parasiticus* in structure and habits suggested that competition might figure in the local distribution of these species. Schaaning (1907) noted that *parasiticus* was common and bred on Novaya Zemlya in 1902, not a lemming year, and the two other species were absent; but in 1903, a lemming year, *pomarinus* and *longicaudus* bred commonly, *parasiticus* was seen but once. Von Jordans (1925) found *pomarinus* and *longicaudus* abundant on Novaya Zemlya in 1924, both apparently breeding, whereas *parasiticus* was not abundant and only a few specimens were taken along the coast. From Taimyr in 1936, Sealon (1938) reports the reverse, *parasiticus* breeding, *pomarinus* not breeding. Popham (1897, 1898, 1901) found all three species of jaegers breeding along the Yenisei River in 1895, as also snowy owls, when lemmings were abundant, but in two subsequent seasons when lemming predators were scarce or absent, only *parasiticus* was breeding. Bertram *et al.* (1934)

ventured to generalize Schaaning's observation as part of their valuable discussion of non-breeding in arctic birds. Our observations and study of the literature support their statements.

In summary, a tentative picture of the breeding distribution and ecological segregation of the three species of jaegers is as follows: The largest and smallest species live on the tundra; both are territorial and depend on lemmings. What overlap in food requirements may occur is mitigated by a habitat separation, with the result that in many areas only one or the other breeds. The intermediate species is more widely distributed than the other two, it is also more versatile, while breeding, in its exploitation of food and in its population organization. It may be a lemming predator, and in certain parts of its breeding distribution, in certain years, would appear to replace *pomarinus* and *longicaudus*. But it tends to give way to these species when lemmings are abundant. Thus, in coastal areas where *pomarinus* and *longicaudus* can breed in good numbers, breeding of *parasiticus* seems to have a strongly opportunistic element, permitted by the periodic non-breeding or low breeding densities of its more narrowly adapted congeners. Whether on this basis alone *parasiticus* could persist as a species is a question not to be answered since such a large part of its breeding populations depends on foods provided by the marine littoral. Nonetheless, the overlap in both ecologic valence and actual distribution around the Arctic Ocean is striking, and it is suggested that this can persist at least in part because of the periodicity of breeding in two species which allows a third and more generalized congener to exploit the intervals.

This hypothesis appears to reconcile much of the available information concerning behavior and distribution of jaegers. While that information is scattered, we venture the hypothesis to emphasize a fundamental question the formulation of which is required if future students in the arctic are to gather data efficiently. What is needed in particular are data on the extent of breeding at any one locality for each of several years, on the basis of which the degree and significance of sympatry among the three species of jaegers can ultimately be determined. Be this as it may, it is clear that the jaegers deserve emphasis as lemming predators fully on a par with other, better known ones. As jaegers become marine in the non-breeding seasons, their role as lemming predators has been underrated in favor of more consistently terrestrial predators like the snowy owl and arctic fox, which are more often encountered by naturalists. There must be long stretches of coastal tundra, such as those illustrated for Taimyr by Birulya (1907), similar to those in northern Alaska where *pomarinus* is an important predator and, indeed, perhaps the most important one.

### 3. INTERSPECIFIC RELATIONS AND THE FACT OF COMPETITION

The aggressive behavior of pomarine jaegers toward other species has been considered briefly. As



the matter of strife among arctic predators is one of primary theoretical importance and one on which only scattered data are available, our observations are reviewed.

Pomarine jaegers were aggressive toward a variety of large birds which trespassed on their territories only incidentally. This aggression, so far as we could detect, could be as strongly manifest toward these other species as to individuals of their own kind. Thus, jaegers of the other two species were chased, as were also glaucous gulls. On June 27, 1953, one bird from each of two neighboring pairs successively chased a gyrfalcon as it flew more or less in a direct line over their territories. On June 28, 1953, a jaeger near plot 3 chased a sandhill crane from there far out over Elson Lagoon.

Relations with owls were basically not different. An owl in flight, either a short-ear or snowy, in the dense population of 1953, rarely escaped the determined attention of one or both members of a pair of territorial jaegers. The owl in flight was harried by repeated swoops of a pair, first one, then the other. Occasional strikes were made by the jaeger, apparently with its feet. A snowy owl would usually drop or swerve suddenly to elude the fast-approaching jaeger or would flip up, with feet more or less raised, causing the jaeger to rise abruptly. In none of these frays was an owl observed actually to grasp or in any way appear to repulse bodily the attack of the jaegers. Short-eareds did not attempt overtly to repulse the attacks, but merely dropped or swerved in flight to avoid them, or climbed up to heights where the jaegers would ignore them.

If grounded, both snowy and short-eared owls could be the focus for dives of the jaegers. This was relatively frequent for the large and conspicuous snowy, rare for the small and inconspicuous short-ear. Again, snowy owls (but not the short ears) usually reacted overtly, repulsing the diving jaegers over them by raising and flapping their wings or actually rising on wing in a sort of hop-flight, meeting the oncoming jaeger directly with a positive gesture of retaliation and calling the bluff, so to speak, of the jaeger, which would then rise quickly. On other occasions the owl merely stooped slightly as the jaeger passed over or it moved a short distance, wobbling ahead, usually down from a mound. On many occasions, jaegers were not so bold as to prompt any of these reactions and in spite of their overhead dives and yelling, the owl would stand impassively.

At no time was a jaeger observed diving over or in any way overtly reacting to an incubating female. The aggression of jaegers toward nesting snowy owls was otherwise intermittent, and although the owls were ignored for long stretches of time if they were grounded, the persistence of the jaegers when owls of either species were on wing led us to suspect that a significant amount of interference occurred. We wondered many times, in 1953, just when and how the owls did their effective hunting. Possibly in the hours of low light, they were less likely to evoke the

reaction of jaegers we describe, but this matter was not investigated. Bailey (1948) reports that Brower saw two pomarine jaegers repeatedly attack and finally kill a snowy owl near its nest. Zhitkov (1912) and Nicholson (1930) also reports conflict between jaegers and owls. Murie (1929) reports jaegers preying on eggs of the snowy owl.

Whereas snowy owls, however much harried by jaegers, held their ground or moved relatively short distances, short-eareds chased by jaegers would take wing and either remain in the general area or, less frequently, fly fairly long distances. In the latter event, the individual short-ear would cross one or several home areas of neighboring short-eareds. A few of these flights extended over a quarter- or even a half-mile. It seems possible that the males were more vulnerable in this respect, as in instances when a female left its nest as a result of disturbance by one of us, it would usually not leave the general area. Once, on June 17, 1953, a short-ear not on a nest took wing near the north end of plot 1, flew southward, and was watched as five pairs of jaegers, one after the other in a chain reaction, took wing and harried the owl, each pair over its own territory. As the aggression of one pair waned near a territorial boundary, the next pair came forward to meet the owl, "escorted" it across, and so on. The neighboring pairs meeting each other near their territorial boundaries also engaged in momentary fracasces among themselves while trying to chase the owl. When the owl was near Wohlschlag Slough, sight of it was lost, and by then it had flown a half-mile easily. Later the same day, a similar sequence of three successive pairs chasing a short-ear was witnessed.

Aggression of other species toward jaegers not provoked directly by annoyance from the latter was seen only a few times. Thus, one of a nesting pair of glaucous gulls watched on June 16, 1953, chased a pomarine jaeger which flew without stopping over a small lake on which the gulls' nest was located. On July 28, 1953, one of a pair of short-eared owls twice flew at a pomarine jaeger which passed through an area where young of the owl were out of the nest. We do not have a single record of a snowy owl deliberately chasing a jaeger. A fracas between a snowy owl and glaucous gulls has been described elsewhere.

Many instances of conflict or competition between predators have been recorded in the voluminous literature on natural history of the arctic. For example, Sutton (1932) reports predation on nests of owls by the arctic fox and a kill of a fox by an owl. Brooks (1915) states that short-eared owls caught in traps were eaten by snowy owls, and Murie (1929) records the short-ear as a prey item for the snowy owl. There are records of attacks on the arctic fox by both the parasitic jaeger (Collett & Nansen 1900) and the long-tailed jaeger (Birulya 1907). Nicholson (1930) reports parasitic jaegers chasing and attacking gyrfalcon, peregrine falcon, and white-tailed sea eagle. However, while showing that incidents of



competition or conflict occur and are striking or dramatic enough to impress an observer, such records are scattered and anecdotal.

More relevant to the question of competition are the facts of territoriality as dealt with in previous sections of this paper. Moreover, in the pomarine jaeger and the short-eared owl, the density of the breeding population can vary severalfold in accordance with the abundance of prey. When we consider the extent of breeding of the pomarine jaeger near Barrow, local nesting failure, nesting losses otherwise as well as the presence of non-breeders through the summer, and when we contrast 1952 with 1953, it is clear that in the latter season, the effort of the population to exploit an area stocked with food was strained and only partly successful.

What makes competition inevitable is the fact that among the over-wintering lemmings exposed in early June by the melt-off of snow, the pregnancy rate is very low or zero (Rausch & Pitelka MS). The abundant supply released for the population of converging predators is therefore bound to fall as little or no replacement is occurring at first. The reproduction which is actively resumed in early June produces a summer generation and this appears in force in mid-July. Evidence on this point will be presented elsewhere. The main point here is that events in the lemming population and its seasonal pattern of significant reproduction is such that where lemmings are abundant as the breeding season of avian predators gets underway, they cannot remain so to sustain the population of predators which appear on the scene in the first few weeks. Hence the drop-off in numbers of jaegers as witnessed in 1952 and 1953 and the partial breakdown of their nesting as witnessed in 1953.

Finally, the tendency toward late nesting effort in a season when lemmings are at peak abundance has already been brought out in the discussion of the nesting cycles of the pomarine jaeger and short-eared owl. It was shown that on the basis of the time available in the short arctic summer, the late nestings are virtually doomed, apart from any imminence of food shortage. While the snowy owl population studied by us was too sparse to provide data on this point, it is clear from Schaaning (1907) that this species can serve as another example. In any event, it is clear that breeding effort in a predator population in the high arctic can spread over a number of weeks in May and June so that irrespective of the fate of late nests because of time factors, the exploitation of prey tends to mount in accordance with its numbers in early summer.

Therefore, the strife among the predator species in general is, in our opinion, a fact. It remains to be determined how intense and how critical it may be in the welfare of the respective populations. We disagree with Lack (1946) who compares the periodic superabundance of *Lemmus* to the seasonal superabundance of insects at mid-latitudes. Predators using the latter are enjoying more or less of a luxury in an area where other resources support at least a minimum of breed-

ing. In northern Alaska and elsewhere in the high arctic where lemming populations support the breeding of predators, Lack suggests that the "foods in question are temporarily so much more abundant than the requirements of their consumers that the latter do not effectively compete with each other while eating them; and . . . this may be true even if the food in question temporarily provides the bulk or even the whole of the diet of the species involved." This is hardly true of such an area as the coastal plain in Alaska and Siberia. Actually Lack was concerned to reconcile the facts of special mid-latitude situations where food was abundant, and competition absent, with Gause's thesis concerning competition; but in referring to the cyclic microtines of the arctic, he assumed food was *superabundant* when actually there is no need for this rationalization and the evidence supports Gause's thesis directly.

#### 4. PREDATION IN RELATION TO POPULATION LEVELS OF LEMMINGS

As was pointed out by Shelford (1943), predators do depress significantly the numbers of lemmings in years when the latter are abundant. Satisfactory documentation for this will consist of systematic data on the pattern of changing population levels in predator and prey simultaneously. We do not have quantitative data of this type on the prey, but our field records leave no doubt in our minds that such depression occurs, and Shelford must have thought likewise when he referred to "positive evidence" on this point. What observations and records can be adduced by us will be presented elsewhere. Here we want only to mention briefly several features of the relation of avian predators to lemmings which bear upon current problems of population ecology.

It appears at first sight that the evidence from the arctic does not agree with the theoretical picture of predator-prey relations advanced by Errington (1946) for mid-latitude populations. The intercompensations that occur in faunistically more complex ecosystems of mid-latitudes suggest that prey taken represents excess individuals and that a basic density of prey controlled by habitat and intraspecific factors survives regardless of predation. But it is clear from densities and weights of avian predators near Barrow (Tables 3 and 4), as well as from available information on food consumption in previous sections, that the summer predator load deals a stupendous blow to the lemming population. It is no exaggeration, and we do not hesitate to estimate, that the mid-July densities of lemmings are the order of 1/10 or even 1/20 of those when the snow melt-off gets well underway in early or mid-June. The true fraction may be smaller yet.

As the population is exposed to this heavy predation only in summer, and as the requirements of these large predators are high, there is no danger of sustained over-exploitation even locally. Moreover, it is not intended here to suggest that predators are or could be responsible for the cyclic downfall of the prey population. It must be understood that the

TABLE 3. Relative abundance of lemming predators near Barrow, Alaska, 1951-53.

Species	1951	1952	1953
Pomarine Jaeger, . . . <i>Stercorarius pomarinus</i>	Uncommon, early summer only; no breeding	Breeding pairs 4/sq. mi.	Breeding pairs 18/sq. mi.
Snowy Owl, . . . . . <i>Nyctea scandiaca</i>	No breeding; scarce	Breeding pairs one/2-4 sq. mi.; few nonbreeders	Breeding pairs one/2-4 sq. mi.; many nonbreeders.
Short-eared Owl, . . . <i>Asio flammeus</i>	No record	One record of one individual	Common; breeding pairs 3-4/sq. mi.
Parasitic Jaeger, . . . <i>Stercorarius parasiticus</i>	Uncommon; no breeding.	Uncommon; one breeding pair.	Scarce; no breeding.
Long-tailed Jaeger, . . <i>Stercorarius longicaudus</i>	Scarce; no breeding.	Scarce; no breeding.	Uncommon; no breeding.
Glaucous Gull, . . . . <i>Larus hyperboreus</i>	Common near ocean shore; scattered breeding inland.	Same	Same
Least Weasel, . . . . <i>Mustela rzioza</i>	No record	No record	Common
Short-tailed Weasel, . <i>Mustela erminea</i>	No record	No record	One record, early summer.
Foxes, . . . . . <i>Alopex lagopus</i> and <i>Vulpes fulva</i>	<i>Alopex</i> rare; no record of <i>Vulpes</i>	Present in small numbers, early winter '52-'53, primarily <i>Alopex</i>	Common in winter '53-'54, both <i>Alopex</i> and <i>Vulpes</i>

TABLE 4. Weights of various birds preying on lemmings.

Species	Number of specimens	Range	Mean	Standard deviation
<i>Stercorarius pomarinus</i>				
Males . . . . .	27	521- 852	682.8 ± 17.2	89.5
Females . . . . .	13	675-1000	828.9 ± 22.5	80.9
<i>Stercorarius parasiticus</i>				
Males . . . . .	11	354- 513	424.0 ± 14.4	47.7
Females . . . . .	6	412- 540	498.8 ± 18.5	45.2
<i>Stercorarius longicaudus</i>				
Males . . . . .	12	201- 305	269.4 ± 9.1	31.4
Females . . . . .	15	287- 353	325.8 ± 5.2	20.3
<i>Larus hyperboreus</i>				
Males . . . . .	15	1137-2250	1514.6 ± 72.4	280.2
Females . . . . .	9	1090-1550	1232.6 ± 51.8	146.1
<i>Asio flammeus</i>				
Males . . . . .	2	260- 300	280	
Females . . . . .	6	328- 475	404.2 ± 24.6	59.1
<i>Nyctea scandiaca</i>				
Males . . . . .	8*	1264-1850	1565.3 ± 74.7	209.3
Females . . . . .	8	1550-2722	2123.7 ± 131.5	370.8

\*Not included is an emaciated adult male found freshly dead at Barrow on June 11, 1951, weighing 1135 gms.

main growth of this population occurs between August of one year and June of the next. In summer, predators reap the main results of this relatively uninhibited population growth. Hence, it appears that

the heavy take of lemmings in the early summer may be a factor in delaying that combination of circumstances which carry the lemming population over a threshold following which a crash occurs. It is difficult to see, in the light of the 1953 scene near Barrow, how the population could have continued to grow through 1952 had predators not intervened. In fact, the crash had been expected in spring, 1953. All aspects of this situation cannot be explored here, but these remarks will suffice to suggest the role of avian predators. They dampen the fluctuations of the prey with respect to both extremes of density reached at any one time and intervals between peak densities. Also, we suggest that the predator-prey situation on an arctic coastal plain both contradicts and supports Errington's thesis. That is to say, the expansion of the lemming population continues in spite of predation, but at least at certain points in the cycle the pattern of that expansion is significantly modified by predation.

Finally, in the ecology of the arctic coastal plain of northern Alaska, the pomarine jaeger is certainly the number one predator of lemmings in the summer and perhaps also on a year-round basis even though predation by this species occurs only in the summer. While known as a lemming predator, the importance of this species in the biology of lemming cycles has been underrated. It is clear that in some parts of the range of this species, lemmings are the sole food supporting large-scale breeding. The fact is that literature examined by us indicates that where pomarine jaegers breed in numbers, they do so in association with an abundance of lemmings.

A basic question posed by the records from Barrow is whether there can be a synchrony of cyclic peaks in lemming populations on a regional basis if the breeding of populations of a predator such as the pomarine jaeger depends on lemmings and if, therefore, the survival of the species depends on them. That so many jaegers can concentrate in an area as that studied by us near Barrow certainly suggests that the regional populations of this species are highly mobile, exploiting local abundances of lemmings as they are located. If such are the circumstances under which the pomarine jaeger breeds, then it seems difficult to see how this species could maintain itself if two- and three-year intervals of nonbreeding were regularly inevitable. We therefore suggest that on the basis alone of evidence regarding avian predators, their numbers and their demands as species, it may prove possible to maintain that the concept of regional synchrony in the lemming cycle is spurious.

The main objective of this paper has been to organize and make available what information we have concerning avian predators and to do this against a background of present-day information and thinking in population ecology. While much previously unavailable data have been collected, it is as painfully clear to us as it will be to many readers that many gaps in our information were left unfilled, and the

confident note struck by the title and table of contents is rather misleading. Perhaps by having gone into various matters somewhat argumentatively we have made clear how very much, by modern standards, has yet to be learned about these predators.

Since field investigators are often persons with academic ties who ordinarily cannot get to the arctic before mid- or late June, there is a point about future study which deserves special emphasis. The briefness of the arctic summer means not only that the breeding cycles of birds must be fitted into the short period available, but that the time over which certain critical events occur at the beginning of the summer is short. Moreover, the early summer melt-off of snow exposes the lemming population after winters with significant population growth, and as this exposure proceeds much of interest and significance is taking place in the predator population. Hence the investigator should be on hand as the bulk of birds arrives, settles, and begins breeding. At Barrow, this time is the last week of May and first two weeks of June.

Few of the opportunities exposed to us by the experience in the arctic are so appealing as that offered by the jaegers. No one person can fully capitalize on it, since research in the field must be conducted at a number of points. But in any one area, and particularly if more than one species breeds there over a period of years, much of value to several different interests in biology can be obtained.

Jaegers are terrestrial gulls, distinct enough that taxonomists have put them in a separate family, but this classificatory circumstance should not cloud the relevance of studies of jaegers to broad problems of phylogeny in gulls, *sensu lato* (as recognized by Ahlquist 1937). To any comparative study of breeding organization in gulls, data from the strongly territorial jaegers will be significant. Also, considering the extensive sympatry of the three terrestrial species in the arctic together with the fact of a closely related maritime species, the great skua (*Stercorarius skua*) of Atlantic and Southern Hemisphere waters, which has a unique bipolar breeding distribution, the genus *Stercorarius* becomes of interest, additionally, from standpoints of distributional history and evolution.

It is as subjects for studies in population ecology, however, that jaegers have their first appeal. They can be watched easily and details of behavior can be gathered confidently. Not only is there a variation in plumage helping the observer to distinguish individuals, but as Daniel Q. Thompson has demonstrated in his work at the Arctic Research Laboratory, jaegers can be trapped easily on the nest and marked with paint so that they are recognizable at considerable distances. Further, the territorial habit, the dimorphism of size and plumage, and the relative distinctness of age groups are features which qualify the jaegers as exceptionally good subjects for population studies. Finally, the dependence of breeding jaegers on lemmings, their distributional sympatry over at least the American arctic, and the ambiguous relations

of the intermediate-sized species (*parasiticus*) to this food source clearly show that particularly through investigations of jaegers, the complex of population interactions associated with lemmings can be studied profitably.

#### SUMMARY

Avian predators common near Barrow, Alaska, at least in some years and preying primarily on lemmings are the pomarine jaeger (*Stercorarius pomarinus*), snowy owl (*Nyctea scandiaca*), and short-eared owl (*Asio flammeus*). Other species preying on lemmings but not on a significant scale are the parasitic jaeger (*Stercorarius parasiticus*), long-tailed jaeger (*Stercorarius longicaudus*), and glaucous gull (*Larus hyperboreus*). Predators were scarce in 1951; but they were present in numbers in the following summers and were censused over 7-9 sq. mi. near Barrow in June and July. In the three year period 1951-53, their densities underwent striking increase. This change followed the upswing portion of the cycle in lemming numbers, which were low in 1951, moderate in 1952, and high in 1953.

Pomarine jaegers did not breed near Barrow in 1951 and occurred sparsely. In 1952 and 1953, breeding densities were 4 and 18 pairs/sq. mi., respectively. In the pomarine jaeger, the nesting cycle lasts 10-11 weeks. The breeding season of 1953 was 10-14 days ahead of that of 1952; also, egg laying occurred over a longer period and breeding activities in general were less synchronized in 1953 than in 1952. Unlike 1952, in 1953 the population included breeding individuals with subadult plumage characteristics. Nesting success was lower in the dense population of 1953 than in the sparse one of 1952. Pomarine jaegers are strongly territorial and remain so throughout the nesting cycle. Each pair occupies an all-purpose territory, as in many passerines. In the densely occupied area of 1953, minimal territory size was estimated at 15-20 ac., where in 1952, territory size on the most densely occupied area was approximately 110 ac.

Snowy owls were uncommon in 1951. In 1952 breeding pairs were present on territories 2-4 sq. mi.; in 1953 the breeding density was not significantly different, but the total number of owls present was higher because of an increase in numbers of non-breeders. The short-eared owl was absent in 1951 and was recorded on only one date in 1952. It was common in 1953; breeding densities reached a maximum of 7 pairs/sq. mi. and the average was no less than 3-4 pairs/sq. mi. Smallest territories were estimated at 50 ac.

The nesting cycle of the snowy owl lasts three months or slightly longer. Clutch size at times of lemming highs averages near seven (range 4-11). The nesting cycle of the short-ear requires 11-12 weeks. Clutch size in the 1953 population averaged near six (range 4-9). Nesting success was low in both species because of interference by jaegers and humans. In neither was there any evidence of second nesting effort following a failure. In the short-ear

fledging success was about 5-10% (owlets taking wing, but still dependent).

The staple food item of these species as breeding birds is the brown lemming, *Lemmus sibiricus*. A young snowy owl maintained in captivity consumed lemmings daily which were equivalent to about 20% of its average weight and required four well-grown lemmings daily. A young short-eared owl maintained in captivity consumed lemmings equivalent to about 35% of its weight and required five moderate-or small-sized lemmings daily. Both owls were in advanced stages of growth and underwent no further marked gains in weight.

Factors affecting the timing and success of breeding of these avian predators in the high arctic environment are length of nesting cycle, inception of molt, early summer drop in prey numbers, and mid-July increase in prey numbers provided by a mid-summer generation.

The reputation of the snowy owl as a lemming predator is secure. The short-eared, while playing a variable role in the lemming cycle, does become an important predator even at 71°N. latitude, at least in Alaska. On the vast coastal plains bordering the Arctic Ocean in North America and Asia, the pomarine jaeger by reason of its numbers may well be the chief lemming predator. It is certainly the chief one in northern Alaska. Habitat and feeding differences separate the three species of jaegers, but considerable overlap between them occurs, and a marked degree of competition between them may prevail because of population shifts provoked by the lemming cycle. Competition also occurs between owls and jaegers. Avian predators successfully depress lemming populations at least in the upswing portion of the cycle to the extent that the fluctuations of the prey are dampened and protracted.

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